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To Sister Rose Angela.  
A. M. May 2, 1881.





BOTANY  
THE SCIENCE









PAINTED FOR THE ENCYCLOPÆDIA BRITANNICA BY ISABEL COOPER AFTER SPECIMENS IN THE NEW YORK BOTANICAL GARDEN

#### COMPOSITE GROUP OF CACTUSES OF NORTH AND SOUTH AMERICA

1. *Cereus Maynardae*, Viscountess Maynard's great-flowering *Cereus*, a hybrid between *Selenicereus grandiflorus*, of the West Indies, and *Heliocereus speciosus*, of Mexico. 2. *Opuntia*, probably *Opuntia vulgaris*, one of the prickly pears of south-eastern South America. 3. *Opuntia basilaris*, a spineless prickly pear, of the south-western United States and northern Mexico. 4.

*Echinocereus* sp., of the western United States and northern Mexico. 5. *Hickenia microsperma*, Professor Hicken's cactus, a native of northern Argentina. 6. *Lobivia cinnabarina*, Cinnabar cactus, found in the Andes of Bolivia. 7. *Cleistocactus smaragdiflorus*, a slender-flowered cactus, native of Argentina.



BRITANNICA BOOKLET No. 10

# BOTANY, THE SCIENCE

A SELECTION OF ARTICLES FROM THE  
NEW 14TH EDITION OF THE

## ENCYCLOPÆDIA BRITANNICA

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WITH FULL PAGE PLATES IN HALFTONE AND COLOUR



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# BOTANY, THE SCIENCE

A SELECTION OF ARTICLES,  
COVERING THE GENERAL AND SYSTEMATIC STUDY OF PLANTS,  
FROM THE NEW 14TH EDITION OF THE  
ENCYCLOPÆDIA BRITANNICA.

## PREFACE

**Plant or Animal?**—Whether that very small individual known to scientists by the name of *Volvox* is an animal or a plant we need not discuss; because, though some call him one and some call him the other, there is little real reason for the difference of opinion. There is no doubt that part of his characteristics are those of animals and part those of plants. You may look upon him as either, and call him what you wish; I mention the disturbing chap simply as an illustration of the fact that in the lower forms there exists little difference between plants and animals; we are led to believe that both have common ancestors in the course of evolution. All life on this planet is, when one regards it from certain viewpoints, surprisingly alike and subject to well-nigh the same vicissitudes. The cells of which plants are constructed are very like those of which man himself is constructed, and these cells are all of the same general kind: a wall inside of which is found that substance known as protoplasm, a more or less colourless, translucent or even transparent and slimy or gelatinous substance allied to the white of egg or the so-called proteins. Inside of this is a cell sap made up of various sugars, nitrogenous materials and inorganic salts and including a nucleus which seems to have to do with the taking in of food, the digesting of it and the reproductive functions. Some of these cells live without aid from others, while some join together to form complicated living beings like the higher plants and man himself, in which case they develop widely different functions suited to the necessities of the whole. In between the two extremes are many varieties of associations, including Colonial Forms both of Algae (the plant forms) and Protozoa (the animal forms). It is interesting to note that not only our little friend *Volvox*, but many of the unicellular plants, as well as animals, can actually swim by the use of an extra bit of their protoplasm delicately elongated to form cilia or arms which push the cell through the water by a movement somewhat like that of the arms of a human being in swimming. Thus we find a surprising development of faculties in even the unicellular life, and upon closer examination we shall be rewarded with more astonishing discoveries.

**Cells.**—*Volvox*, for instance, has an eye-spot already developed, but let us examine more closely some of the typical plant cells. We find that protoplasm is in some mysterious way associated with life, and that protein is also associated with protoplasm. Within this protoplasm there seems to take place an enormous number of chemical reactions, and the peculiar co-ordination of these processes, which mark the living cell, are in some way related to the colloidal nature (see Colloids in the *Encyclopædia Britannica*) of the protoplasmic substratum in which they occur. The physical relationship of this colloidal protoplasm in the cell is certainly far more complex than that of any colloidal material studied in the laboratory. Other substances of more or less unknown nature found in the cells are the Enzymes, of which we do know three marked characteristics: (1.) they can act as catalytic agents; (2.) they act in very minute quantities and do not appear themselves to be used up in the process; (3.) they are very sensitive to heat. It must also be noted that the processes they accelerate may be either those of breaking down or those of building up (synthetic). These complicated little chemical laboratories called cells, in which the mystery of life is centred, must be swollen with water in order to carry on their functions, and it is the protoplasm which lets water pass readily in or out without permitting the other substances to do so; and so much water is needed that, in lettuce and beet leaves, for instance, there is something like 90% water. It is due to this inflation of the cells that some plants have a rigidity far greater than could be expected from their actual mechanical strength. Thus, when a flower wilts, it is from exhaustion of the water in its cells which collapse like small balloons and cause the stem to lose its rigidity.

**Distinguishing between Plants and Animals.**—I have pointed out that all life has much in common. Wherein, then, does a plant differ from an animal? Perhaps you have been under the impression that the difference may be based upon movement; a tree is rooted to one spot while an animal can move about. On the contrary we have found that there are many plants which



can move or propel themselves. There are others, such as the insectivorous plant, Venus's Fly-Trap, which has leaves, "each leaf has two lobes, standing at rather less than a right angle to each other, their edges being produced into spike-like processes. The upper surface of each lobe is covered with minute circular sessile glands. It bears also three fine-pointed sensitive bristles. These contain no fibro-vascular bundles, but show a constriction near their bases, which enables them to bend parallel to the surface of the leaf when the lobes close. When the bristles are touched by an insect the lobes—after a latent period of less than a second under suitable temperature conditions—close upon the hingelike midrib, the spikes interlock, and the insect is imprisoned." Thus there are not only plants which swim, but there are plants which seem to be able to shut their leaves like claws upon unfortunate insects which are then digested and converted into food for the capturer. It would seem that our idea of a plant as something that is set in a fixed place, is somewhat misleading in its suggestion of lack of ability to move. Another division which has been suggested is that of feeling; it has been said that animals are sentient beings while plants are not, but very interesting recent experiments seem to prove beyond a doubt that plants do, in a sense, feel and react to their feelings. Let us quote *The Century Dictionary*: "While the difference between plants and animals in all their higher forms is clearly marked, science has hitherto been unable to fix upon any one absolutely universal criterion between them. Nothing is perhaps so distinctive of the plant as its power to appropriate and assimilate mineral matter directly, whereas most animals live on the products of previous organization. . . . But many plants, including the whole group of fungi, and the saprophytic, parasitic and carnivorous flowering plants, live wholly or in part on organic matter, while not all animals are confined to organic nutriment." You will find this subject very fully treated in the *Encyclopædia Britannica*.

**Plant Functions.**—In the article on Plants in the *Britannica*, reprinted in this booklet, will be found the statement that "The whole life of the globe is dependent on this photosynthetic power of green plants, for they alone are able to manufacture food material for themselves. The green plant may be described as the great alchemist which alone of living things has mastered the secret of converting the sun's rays into food material." In this same article you will read of the wonderful processes of absorption of the necessary salts; of the strangely efficient cell which can exclude certain salts and store others, to the extent found in the *Valonia*, a seaweed which upon analysis shows a concentration of potassium of 40 times that of the sea water in which it is found; of Chlorophyll and the other pigments which absorb some of the light of the sun and make use of its energy to decompose carbon dioxide; and you will be told how sugar is formed and much more of the strange faculty of converting the sun's rays

into food, which more than anything else differentiates the life of the vegetable kingdom from that of the animal. All of this has to do with the general metabolism of the plant, and the process is very much the same in the green Algae as it is in the more highly developed flowers and trees.

**Seed Bearing Plants.**—Let us now look for a little into the structure and life of some of those higher types which we know better for having seen many times during our lives. All living seed-bearing plants are divided into two groups: the Gymnosperms or plants having their seeds naked and the Angiosperms or plants having their seeds wholly enclosed in an ovary or container. The first type is very old; the second was a much later development on the earth. The first type is represented by pines, spruces, cedars and other evergreens, and it is interesting to note that the Chinese, thousands of years ago, imputed great age to these trees and in fact used them to symbolize long life and the wisdom of the ancients.

The Angiosperms are represented by the flowering plants. They are the highest form, and at present the dominant vegetation on the earth's surface. They also occur abundantly in the shallows of rivers and freshwater lakes and in the sea; such aquatic angiosperms are not, however, primitive forms, but are derived from immediate land ancestors. They comprise plants as far apart as are the duckweed, a tiny green shoot without distinction of root, stem and leaf, and the great forest tree with its complicated anatomy of roots, trunk and huge spread of branches, twigs and leaves. Between these two is every conceivable variation of creeping, erect or climbing shrub or tree. In rare cases the plant is quite simple and the axis unbranched as in the tulip which has scale leaves on the underground bulb, green foliage leaves and coloured floral leaves all on the same stem, but generally the flowers are formed only on shoots of a higher order, often only on the ultimate branches of a much branched system, and occasionally leaf-buds arise from the roots as in fruit trees, poplars, elms and others. And then, quoting a little farther on, we come to one of the most interesting facts of all:—"The flower on all of these plants is nothing more than a shoot (a stem bearing leaves) with a special form associated with the function of ensuring the fertilization of the egg and the development of fruit containing seed. *It is for this reason that so much can be done to change the form of this flower which is nothing more after all than specially and more or less recently developed leaves.*"

**Transmutation of Parts.**—I shall let you read for yourself the details of the ways that seeds are protected, and all of the varied means of pollination which are found among the Angiosperms. Let us consider rather the marvellous adaptation and transmutation of parts which plants seem to have and which these higher orders seem to have carried to an almost unbelievable extent. Man has two arms and two legs; seldom is he born with more; yet a tree may have almost unlimited



branches and is only stopped in the development of them because of their weight, of the necessity of supplying them with food and other such outside reasons. We are perhaps in the habit of thinking that roots are used for certain purposes, the stem or trunk for another and the leaves for others, and that each have, as it were, well defined jobs to perform. We find, however, that ivy clings with rootlets, bryony, the passion flower and others with their stems, and clematis and grapes with leaf tendrils. Thus plants make use of each of their major parts to function in climbing, and as we shall see in other functions also.

**Roots.**—I shall list just a few of the examples of interesting information about roots, of which you will find many more as you pursue your reading: Begonia leaves when placed in soil can give rise to roots; some leafless orchids depend for nourishment entirely upon their roots, which perform the functions both of leaves and roots; certain mangroves growing in swampy soil or water send vertical roots up into the air which provide passages for air into the root system below; and some plants actually get along with no roots at all.

**Stems.**—Stems are quite as interesting: Some are subterranean; prickly-pear stems become fleshy and green and perform the functions of leaves, as well as being water reservoirs, for the plants and the leaves are reduced to spines; the potato is a stem with leaf buds, the eyes, only it is somewhat thickened. The bulb is just another form of stem with leaves on it.

**Leaves.**—But of all the parts of plants, the leaves are undoubtedly the most adaptable and varied in their functions. Investigation has shown that many parts of the plant which appear quite different from ordinary leaves are in truth very similar to them and in fact their morphological equivalents. Leaves are frequently transformed into tendrils, as in the leguminous plants (the pea tribe). The wonderfully complicated pitchers of some insectivorous plants are composed of one or more leaves. There are also underground leaves. But it is when one stops to study the intricate transformation that has taken place in leaves to form flowers that the full marvel is found; the scent, the clever arrangements for the luring of insects which are made to carry the pollen, and the protection of all that takes place in the development of the fruit and seed are found to involve so many unexpected inventions that the student feels again the wonder of nature, the great experimenter. (See the preface to the booklet on *Fishes, Insects and Reptiles* in this series.)

**Seed Distribution.**—After the flower has performed its life work and is faded and gone, there still remains the necessity to distribute the seeds to some little distance so that the species may survive and multiply. We have all seen winged seeds and hooked seeds which attach themselves to the fur of animals and the feathers of birds and are carried in this way for great distances, but did you know that the Rose of Jericho develops its fruits and then dies, drying up into a mass easily

rolled over the ground by the wind, that the mistletoe develops a sticky layer around the seeds which cling to the bills of birds eating the berries and are wiped off on the bark of other trees and thus the embryo is transported to a new host; and that the gorse shoots its seeds out by splitting and curling the pod in which they are contained and that they must then be buried by ants in order to germinate?

**Nature's Struggle.**—Many are the struggles to survive and varied are the ways of meeting the ever changing conditions of environment. It is stated in the article on Plants in this booklet, "Careful observation shows that, quite apart from the periodic rhythm of the seasonal changes, no community is stable." This is because some are being choked out, others are finding the encroachments of man, mammal or insect too strong for endurance, others have been eliminated through climatic changes, and so on and so on, for the strong survive and the weak or those unfitted to adapt themselves to the imposed changes are lost. We find that plants like animals are made of cells. We find that these cells are much alike and that there is strong reason to believe that aeons ago both sprang from a common ancestor. We see that the vegetable world is as changing as is the animal, though its changes may in some instances be far longer in taking place. We have noted that these changes are forced by the ever changing environment and a brief reading of palaeobotany will convince us that those types which could not keep pace with the change of things were lost to this world for ever. Here again we are confronted, as in zoology, as in astronomy, and, in truth, as in every natural science, with the restlessness of nature and with the insecurity of all things. All is movement; it is a question of swim or sink.

Teachers and students should bear in mind this struggle for existence and ask themselves, as I have suggested, the whys and wherefores of things. A lot of unrelated facts are not interesting any more than is a jumbled picture puzzle; if they begin to fit together and one discovers some little idea of the design, the thing becomes fun; it is then that one feels real interest in all that is going on about us in this world, an interest that brings a reward well worth the effort.

This book is diverse in authorship and of undoubted authority. Both are good points in its favour. The diversity guarantees a broad and unbiased viewpoint so necessary to understanding. The security of undoubted authority is not easily discovered. The men who have written the articles in this book, and in all the volumes of the New 14th Edition of the *Encyclopædia Britannica*, are recognized throughout the civilized world as masters, each in his own field.

There is in this series another book on Botany which gives articles on each individual plant as well as long, practical articles on Horticulture, Landscape Architecture, Japanese Gardens and many more subjects. That is what may be called the practical man's book; it is

for him who would know the names of wild flowers and trees or who wishes to grow flowers or make a vegetable garden; that book is necessary to the student who uses this book, for the two dovetail perfectly.

And now I shall leave you to set out upon your exploration; to find out how a 300-foot tree gets gallons of water up to its branches and proportions it to each leaf every day; how plants push their stems up against

gravity and their roots downward into the hard soil; how they turn their heads towards the light; how some of the less known methods of pollination take place, and a score of other fascinating things which will make you look at every green and growing thing and every piece of seaweed from now on with different eyes.

WARREN E. COX

#### PUBLISHERS' NOTE

Since the publication of the New 14th Edition of the Encyclopædia Britannica, we have received thousands of requests to publish in separate form the articles in certain fields of knowledge so that these articles may be the more available for continuous reading, for students' use, etc. Accordingly we have prepared booklets containing all the Britannica articles on Painting; Mammals and Birds; Chinese Art; Botany: Plants and Gardening; The Earth, the Seas and the Heavens; Japanese Art; Fishes, Reptiles and Insects; The Theatre and Motion Pictures; Graphic Arts; and expect to follow these with many others. We trust they will prove useful, not only in themselves but also as evidence of the wide scope and the fullness of information in the Britannica itself.

The articles in this booklet are all taken *verbatim* from the New 14th Edition of the Encyclopædia Britannica except that material not essential to the subject has been omitted and in a few unimportant instances certain material has been condensed for mechanical reasons. The plates, too, are reproduced unchanged but the numbering is not always consecutive because the original numbering has been retained in order to agree with the text. A number of cross references to articles not in this booklet have also been retained for the benefit of those who possess the Britannica.

Following the Britannica custom, we have retained at the end of signed articles, the initials and not the full name of the author. The reader, however, can always identify the author by referring to the List of Contributors where the full names of the authors are given together with their initials.



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BOTANY  
THE SCIENCE



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A SELECTION OF ARTICLES FROM THE NEW 14TH EDITION OF THE  
ENCYCLOPÆDIA BRITANNICA

**B**OTANY, the science which includes everything relating to the vegetable kingdom, whether in a living or in a fossil state. The name is derived from the Greek *βοτάνη*, a plant. It embraces a consideration of the external forms of plants—of their anatomical structure, however minute—of the functions which they perform—of their classification—of their distribution over the globe at the present and at former epochs—and of the uses to which they are subservient. It examines the plant in its earliest state of development, and follows it through all its stages of progress until it attains maturity. It takes a comprehensive view of all the plants which cover the earth, from the minutest organism, only visible by aid of the microscope, to the tall forest tree. It marks the relations which subsist between all members of the plant world, including those between existing groups and those known only from their fossilized remains preserved in the rocks. We deal here with the history and evolution of the science.

**Descriptive Botany to the Time of Linnaeus.**—The plants which adorn the globe more or less in all countries have attracted the attention of mankind from the earliest times. Solomon “spake of trees, from the cedar of Lebanon to the hyssop on the wall.” The Chaldaeans, Egyptians and Greeks were the early cultivators of science, and botany was not neglected, although the study of it was mixed up with crude speculations as to plant life, and as to the change of plants into animals. About 300 B.C., Theophrastus wrote a history of plants, and described about 500 species used for the treatment of diseases. Dioscorides, a Greek botanist and a physician in the Roman Army, wrote on *Materia Medica*; his contemporary, the elder Pliny (A.D. 23–79) described about a thousand plants, many of them famous for their medicinal virtues. Asiatic and Arabian writers also took up this subject. Little, however, was done in the science of botany, properly so called, until the 16th century, when the revival of learning dispelled the darkness which had long hung over Europe. Otto Brunfels, a physician of Bern, has been looked upon as the restorer of the science in Europe. In his *Herbarium*, printed at Strassburg (1530–36), he gave descriptions of a large number of plants, chiefly those of central Europe, illustrated by beautiful woodcuts. He was followed by other writers—Leonhard Fuchs, whose *Historia Stirpium* (Basel, 1542) is worthy of special note for its excellent woodcuts; Hieronymus Bock, whose *Kreutter Buch* appeared in 1539; and William Turner, “The Father of English Botany,” the first part of whose *New Herbal*, printed in English, was issued in 1551. The descriptions in these early works were encumbered with much medicinal detail, including speculations as to the virtues of plants. Plants which were strikingly alike were placed together, but there was at first little attempt at systematic classification. A crude system, based on the external appearance of plants and their uses to man, was gradually evolved, and is well illustrated in the *Herbal*, issued in 1597 by John Gerard (1545–1612), a barber-surgeon, who had a garden in Holborn.

One of the earliest attempts at a methodical arrangement of plants was made in Florence by Andreas Caesalpinus (1519–1603). In his work *De Plantis* (1583), he distributed the 1,520 plants then known into fifteen classes, the distinguishing characters being taken from the fruit.

The Englishman John Ray (1627–1705) did much to advance the science of botany, and was also a good zoologist. He promulgated a system which may be considered as the beginning of a natural system (*Methodus Plantarum*, 1682). He separated flowering from flowerless plants (ferns, mosses, seaweeds, fungi, etc.) and divided the former into Dicotyledons (with a pair of seed-leaves) and Monocotyledons (with a single seed-leaf). His orders (or “classes”) were founded to some extent on a correct

idea of the affinities of plants, and he far outstripped his contemporaries in his enlightened views of arrangement.

In 1669 Robert Morison<sup>1</sup> (1620–83), the first professor of botany at Oxford, published a systematic arrangement of plants, largely on the lines previously suggested by Caesalpinus. He divided them into eighteen classes, distinguishing plants according as they were woody or herbaceous, and taking into account the nature of the flowers and fruit. In 1690 Rivinus<sup>2</sup> promulgated a classification founded chiefly on the forms of flowers. J. P. de Tournefort<sup>3</sup> (1656–1708), who about the same time took up the subject of plant-classification, was long at the head of the French school of botany, and published a systematic arrangement in 1694–1700. He described about 8,000 species of plants, and distributed them into 22 classes, chiefly according to the form of the corolla, distinguishing herbs and under-shrubs on the one hand from trees and shrubs on the other. Tournefort’s system was for a long time adopted on the Continent, but was ultimately displaced by that of Carl von Linné, or Linnaeus (1707–78, *q.v.*).

**Linnaean System of Classification.**—The System of Linnaeus was founded on characters derived from the stamens and pistils, the so-called sexual organs of the flower, and hence it is often called the sexual system. It is an artificial method, because it takes into account only a few marked characters in plants, and does not propose to unite them by natural affinities. It is an index to a department of the book of nature, and as such is useful to the student. It does not aspire to any other character, and although it cannot be looked upon as a scientific and natural arrangement, still it has a certain facility of application which at once commended it. It does not of itself give the student a view of the true relations of plants, but by leading to the discovery of the name of a plant it is a stepping-stone to the natural system. Linnaeus himself regarded it as only a temporary convenience and in his *Fragmenta* published in his *Philosophia Botanica* (1751) endeavoured to arrange the genera he had already established according to their affinities under 67 orders.

The Linnaean system was strongly supported by Sir James Edward Smith (1758–1828), who adopted it in his *English Flora*, and who also became possessor of the Linnaean collection. The system was for long the only one taught in the schools of Britain, even after it had been discarded by those in Continental countries.

**The French School.**—A new era dawned on botanical classification with the work of Antoine Laurent de Jussieu (1748–1836). His uncle, Bernard de Jussieu, had adopted the principles of Linnaeus’s *Fragmenta* in his arrangement of the plants in the royal garden at the Trianon. At an early age Antoine became botanical demonstrator in the Jardin des Plantes, and was thus led to devote his time to the science of botany. Having to arrange the plants in the garden, he followed the lines already suggested by his uncle, and developed a system founded in a certain degree on that of Ray, in which he adopted the simplicity of the Linnaean definitions, and displayed the natural affinities of plants. His *Genera Plantarum*, begun in 1778, and published in 1789, was an important advance, and formed the basis of all natural classifications. One of the early supporters of this natural method was Augustin Pyramus de Candolle (1778–1841), who in 1813 published his *Théorie élémentaire de la botanique*, in which he showed that the affinities of plants are to be sought by the comparative study of the form and development of organs (morphology), not of their functions (physiology). His *Prodromus Systematis Naturalis Regni Vegetabilis* was intended to be an arrangement and

<sup>1</sup>R. Morison, *Praeludia Botanica* (1669); *Plantarum Historiae Universalis Oxon.*, pars secunda (1680).

<sup>2</sup>Rivinus (Augustus Quirinus) paterno nomine Bachmann, *Introductio generalis in Rem Herbarium* (Lipsiae, 1690).

<sup>3</sup>J. P. de Tournefort, *Eléments de botanique* (1694); *Institutiones Rei Herbariae* (1700).



description of all known plants. This work was continued after his death, by his son Alphonse de Candolle, with the aid of other eminent botanists, and embraces descriptions of the genera and species of the families of Dicotyledons. The system followed by de Candolle is a modification of that of Jussieu.

In arranging plants according to a natural method, we require a thorough comparative knowledge of the form and structure of plant-organs and hence the advances made in these departments have materially aided the efforts of systematic botanists.

**British and German Schools.**—Robert Brown (1773–1858) was the first British botanist to support and advocate the natural system of classification. The publication of his *Prodromus Florae Novae Hollandiae* (in 1810), according to the natural method, led the way to the adoption of that method in the universities and schools of Britain. In 1827, Brown announced his important discovery of the distinction between angiosperms and gymnosperms, and the philosophical character of his work led Alexander von Humboldt to refer to him as *Botanicorum facile princeps*. In 1830, John Lindley published the first edition of his *Introduction to the Natural System of Botany* embodying a slight modification of de Candolle's system. From the year 1832 up to 1859 great advances were made in systematic botany, both in Britain and on the Continent of Europe. The *Enchiridion* and *Genera Plantarum* of S. L. Endlicher (1804–49), the *Prodromus* of de Candolle, and the *Vegetable Kingdom* (1846) of J. Lindley became the guides in systematic botany, according to the natural system.

The least satisfactory part of all these systems was that concerned with the lower plants or cryptogams, *i.e.*, plants without an obvious flower producing a seed, as contrasted with the higher or flowering plants (phanerogams). The development of the compound microscope rendered possible the accurate study of their life-histories; and the publication, in 1851, of the results of Wilhelm Hofmeister's researches on the comparative embryology of the higher Cryptogamia shed a flood of light on their relationships to each other and to the higher plants, and supplied the basis for the distinction of the great groups in ascending order ThallopHYTA (seaweeds, fungi, lichens) Bryophyta (mosses), Pteridophyta (ferns) and Phanerogamae (seed-bearing plants) the last named including Gymnospermae (seeds not enclosed in a fruit) and Angiospermae (seeds enclosed in a fruit).

Charles Darwin's *Origin of Species* (1859) and the consequent theory of evolution suggested a new point of view for botanists. It became evident that a natural system of classification should present not only existing relationships of plant-families but also their past relationships; a perfect system should be a genealogical tree representing the story of plant-life from its remote origin. But plant-families at the present day represent only the end branches of a great tree most of which has disappeared and the reconstruction of which with the aid of the fragments that have been preserved in the rocks must be a matter of conjecture. The study of phylogeny, *i.e.*, the reconstruction of the genealogical tree, has received much attention from botanists in recent years, some account of this will be found in the articles on the various groups GYMNOSPERMS, ANGIOSPERMS, etc.

**Anatomy of Plants.**—The study of the anatomy and physiology of plants did not keep pace with the advance in classification. Nehemiah Grew and his contemporary, Marcello Malpighi, were the earliest discoverers in the department of plant anatomy. Both authors laid an account of the results of their study of plant structure before the Royal Society of London almost at the same time in 1671. Malpighi's complete work, *Anatome Plantarum*, appeared in 1675 and Grew's *Anatomy of Plants* in 1682. Then for more than a hundred years the study of internal structure was neglected. In 1802 appeared the *Traité d'anatomie et de physiologie végétales* of C. F. B. de Mirbel (1776–1854), which was quickly followed by other publications by Kurt Sprengel, L. C. Treviranus (1779–1864), and others. In 1812, J. J. P. Moldenhauer isolated cells by maceration of tissues in water. The work of F. J. F. Meyen and Hugo von Mohl in the middle of the 19th century placed the study of plant anatomy on a more scientific basis. Reference must also be made to M. J. Schleiden (1804–81) and F. Unger (1800–70), while in Karl von Nägeli's investi-

gations on molecular structure and the growth of the cell membrane we recognize the origin of modern methods of the study of cell-structure included under cytology (*q.v.*). The work of Karl Sanio and Theodor Hartig advanced knowledge on the structure and development of tissues, while Anton de Bary's *Comparative Anatomy of the Phanerogams and Ferns* (1877) supplied an admirable presentation of the facts so far known. This work was made available for English readers in the translation by F. O. Bower and D. H. Scott (1884) and may be regarded as the beginning of the modern era of the study of the general arrangement of plant-tissues (anatomy) and the detailed structure of the tissues themselves (histology) which have been pursued by numerous workers in Great Britain, France, Germany and America, and in which the study of the structure of fossil plants has played an important part. This is treated in full in the article PLANTS: *Anatomy of, Modern Progress of the Subject*.

**Fertilization.**—The subject of fertilization was one which early excited attention. The idea of the existence of separate sexes in plants was entertained in early times, long before separate male and female organs had been demonstrated. The production of dates in Egypt, by bringing two kinds of flowers into contact, proves that in very remote periods some notions were entertained on the subject. Female date-palms only were cultivated, and wild ones were brought from the desert in order to fertilize them. Herodotus informs us that the Babylonians knew of old that there were male and female date-trees, and that the female required the concurrence of the male to become fertile. This fact was also known to the Egyptians, the Phoenicians and other nations of Asia and Africa. The Babylonians suspended male clusters from wild dates over the females; but they seem to have supposed that the fertility thus produced depended on the presence of small flies among the wild flowers, which, by entering the female flowers, caused them to set and ripen. The process was called palmification. Theophrastus, who succeeded Aristotle in his school in 322 B.C., frequently mentions the sexes of plants, but he does not appear to have determined the organs of reproduction. Pliny (A.D. 23–79) speaks particularly of a male and female palm, but his statements were not founded on any real knowledge of the organs. From Theophrastus down to Caesalpinus, who died at Rome in 1603, there does not appear to have been any attention paid to the reproductive organs of plants. Caesalpinus had his attention directed to the subject, and he speaks of a halitus or emanation from the male plants causing fertility in the female.

Nehemiah Grew seems to have been the first to describe, in a paper on the *Anatomy of Plants* read before the Royal Society in November 1676, the functions of the stamens and pistils. Grew speaks of the *attire*, or the stamens, as being the male parts, and refers to conversations with Sir Thomas Millington, Sedleian professor at Oxford, to whom the credit of the sexual theory seems really to belong. Grew says that "when the attire or apices break or open, the globules or dust falls down on the seedcase or uterus, and touches it with a prolific virtue." Ray adopted Grew's views, and states various arguments to prove their correctness in the preface to his work on European plants, published in 1694. In the same year R. J. Camerarius, professor of botany and medicine at Tübingen, published a letter on the sexes of plants, in which he refers to the stamens and pistils as the organs of reproduction, and states the difficulties he had encountered in determining the organs of cryptogamic plants. In 1703, Samuel Morland, in a paper read before the Royal Society (*Phil. Trans.* xxiii., 1474) stated that the farina (pollen) "is a congeries of seminal plants, one of which must be conveyed into every ovum before it can become prolific." In this remarkable statement he seems to anticipate in part the discoveries afterwards made as to pollen tubes. In 1711, E. F. Geoffroy, in a memoir presented to the Royal Academy at Paris, supported the views of Grew and others as to the sexes of plants (*Mém. Acad. Roy. Sci.*, 1711, 207). He states that the germ is never to be seen in the seed till the apices (anthers) shed their dust; and that if the stamina be cut out before the apices open, the seed will either not ripen, or be barren if it ripens. He mentions two experiments made by him to prove this—one by cutting off the staminal flowers in maize, and the



other by rearing the female plant of *mercurialis* apart from the male. In these instances most of the flowers were abortive, but a few were fertile, which he attributes to the dust of the apices having been wafted by the wind from other plants.

Linnaeus took up the subject in the inauguration of his sexual system. He divided plants into sexual and asexual, the former being phanerogamous or flowering, and the latter cryptogamous or flowerless. In the latter division of plants he could not detect stamens and pistils, and he did not investigate the mode in which their germs were produced. He was no physiologist, and did not promulgate any views as to the embryogenic process. His followers were chiefly engaged in the arrangement and classification of plants, and while descriptive botany made great advances the physiological department of the science was neglected. His views were not, however, adopted at once by all, for we find Charles Alston stating arguments against them in his *Dissertation on the Sexes of Plants* (1754); (See *Essays and Observations, Physical and Literary*; Medical Society of Edinburgh, i., 205 [1754]). Alston's observations were founded on what occurred in certain unisexual plants, such as *mercurialis*, spinach, hemp, hop and bryony. The conclusion at which he arrives is that the pollen is not in all flowering plants necessary for impregnation, for fertile seeds can be produced without its influence. He supports parthenogenesis in some plants. Soon after the promulgation of Linnaeus's method of classification, the attention of botanists was directed to the study of cryptogamic plants, and the valuable work of Johann Hedwig (1730-99) on the reproductive organs of mosses made its appearance in 1782. He was one of the first to point out the existence of certain cellular bodies in these plants which appeared to perform the functions of reproductive bodies, and to them the names antheridia and pistillidia were given. This opened up a new field of research, and led the way in the study of cryptogamic reproduction, which has since been much advanced by the labours of numerous workers. The interesting observations of Morland, already quoted, seem to have been neglected, and botanists were for a long time content to know that the scattering of the pollen from the anther, and its application to the stigma, were necessary for the production of perfect seed, but the stages of the process of fertilization remained unexplored, and no one attempted to raise the veil which hung over the subject of embryogeny.

In 1815, L. C. Treviranus, professor of botany in Bonn, roused the attention of botanists to the development of the embryo, but although he made valuable researches, he did not add much in the way of new information. In 1823, G. B. Amici discovered the existence of pollen-tubes, and he was followed by A. T. Brongniart (1801-76) and Robert Brown. The latter traced the tubes as far as the nucleus of the ovule. These important discoveries mark a new epoch in embryology, and may be said to be the foundation of the views now entertained, which were materially aided by the subsequent elucidation of the process of cytogenesis, or cell-development, by Schleiden, Schwann, Mohl and others. The whole subject of fertilization and development of the embryo has been more recently investigated with great assiduity and zeal, as regards both cryptogamous and phanerogamous plants, and details must be sought in the various special articles. The observations of Darwin as to the fertilization of orchids, *Primula*, *Lythrum*, and other flowering plants, and the part which insects take in this function, gave an explanation of the observations of Christian Konrad Sprengel, made at the close of the 18th century, and opened up a new phase in the study of botany, which has been followed by Hermann Müller, Federico Delpino and others. This phase of the subject, the transference of the pollen from the stamens to the stigma of the flower, is now distinguished as pollination, the term fertilization being restricted to the processes directly associated with the union of the male and female cells which occurs in all plant-groups. (An excellent handbook is Paul Knuth's *Handbook of Pollination*, Eng. trans., 1906-09.)

**Physiology of Plants.**—One of the earliest workers at plant physiology was Stephen Hales. In his *Vegetable Statics* (1727) he gave an account of numerous experiments and observations which he had made on the nutrition of plants and the movement of sap. He showed that the gaseous constituents of the air con-

tribute largely to the nourishment of plants, and that the leaves are the organs which elaborate the food; the importance of leaves in nutrition had been previously pointed out by Malpighi in a short account of nutrition which forms an appendix to his anatomical work. The birth of modern chemistry in the work of J. Priestley and A. L. Lavoisier, at the close of the 18th century, made possible the scientific study of plant-nutrition, though Jan Ingenhousz in 1779 discovered that plants incessantly give out carbonic acid gas, but the green leaves and shoots only exhale oxygen in sunlight or clear daylight, thereby indicating the distinction between assimilation of carbonic acid gas (photosynthesis) and respiration. N. T. de Saussure (1767-1845) gave precision to the science of plant-nutrition by use of quantitative methods. The subjects of plant-nutrition and respiration were further studied by R. J. H. Dutrochet towards the middle of the century, and J. von Liebig's application of chemistry to agriculture and physiology put beyond question the parts played by the atmosphere and the soil in the nutrition of plants.

The phenomena of movements of the organs of plants attracted the attention of John Ray (1693), who ascribed the movements of the leaf of *mimosa* and others to alteration in temperature. Linnaeus also studied the periodical movements of flowers and leaves, and referred to the assumption of the night-position as the sleep-movement. Early in the 19th century, Andrew Knight showed by experiment that the vertical growth of stems and roots is due to the influence of gravitation, and made other observations on the relation between the position assumed by plant organs and external directive forces, and later Dutrochet, H. von Mohl and others contributed to the advance of this phase of plant physiology. Darwin's experiments in reference to the movements of climbing and twining plants, and of leaves in insectivorous plants, opened up a wide field of enquiry as to the relation between plants and the various external factors, which has attracted numerous workers. By the work of Julius Sachs and his pupils plant physiology was established on a scientific basis, and became an important part of the study of plants, for the development of which reference may be made to the article *PLANTS: Physiology*. The study of form and development has advanced under the name morphology, with the progress of which are associated the names of K. Goebel, Eduard Strasburger, A. de Bary, F. O. Bower and others (see *PLANTS: Morphology*), while more recently, as cytology (*q.v.*), the intimate study of the cell and its contents has attracted considerable attention.

**Geographical Botany.**—The department of geographical botany made rapid advance by means of the various scientific expeditions which have been sent to all quarters of the globe, as well as by individual effort, since the time of A. von Humboldt (see *PLANTS: Distribution and Ecology*). The question of the mode in which the floras of islands and of continents have been formed gave rise to important speculations by such eminent botanical travellers as Charles Darwin, Sir J. D. Hooker, A. R. Wallace, H. B. Guppy and others. The connection between climate and vegetation has also been studied. Quite recently, under the name of ecology, the study of plants in relation to each other and to their environment has become the subject of systematic investigation.

**Study of Fossil Plants.**—The subject of palaeontological botany (see *PALAEOBOTANY*) has been advanced by the researches of both botanists and geologists. The nature of the climate at different epochs of the earth's history has also been determined from the character of the flora. The works of A. T. Brongniart, H. R. Goeppert and W. P. Schimper advanced this department of science. Among others who contributed valuable papers on the subject may be noticed Oswald Heer, who made observations on the Miocene flora, especially in Arctic regions; Gaston de Saporta, who examined the Tertiary flora; William Carruthers who studied the fossil Gymnosperms; Sir J. W. Dawson and Leo Lesquereux, and others who reported on the Canadian and American fossil plants. In Great Britain also W. C. Williamson, by his study of the structure of the plants of the coal-measures, opened up a new line of research which has been followed by Robert Kidston, Bertrand Renault, D. H. Scott, A. C. Seward, G. R. Wieland, C. R. Zeiller and others, and has led to important discoveries on



the nature of extinct groups of plants and also on the phylogeny of existing groups.

**Study of Diseases of Plants.**—Plant-pathology or the study of the diseases to which plants are subject, more especially under the frequently unnatural conditions attending cultivation, originated as a science mainly in the work of Anton de Bary on the life-history of those fungi which live parasitically on other plants (*Comparative Morphology of the Fungi, Mycetozoa and Bacteria*, Eng. trans., 1887). The science was developed by A. B. Frank and P. C. M. Sorauer in Germany, Marshall Ward in England and others, and the subject is becoming increasingly important from an economic point of view (see PLANTS: *Pathology*). A recent development has been the establishment of bureaux and institutes of Mycology for the study of diseases caused by fungi and the diffusion of information on the subject.

**Study of Heredity.**—The work of the Abbé Mendel in Moravia on the laws governing the transmission of characters in plant-breeding has during the last thirty years given rise to a new department of study, genetics (*q.v.*), in the development of which William Bateson took a leading part. This new development is of importance not only from a scientific aspect as throwing light on the problems of heredity (*q.v.*) but also economically from its relation to plant-breeding (*q.v.*).

**Subdivisions.**—Botany may be divided into the following departments:—

1. Structural, having reference to the form and structure of the various parts, including (*a*) Morphology, the study of the general form of the organs and their development—to be found treated in detail in a series of articles dealing with the great subdivisions of plants (see ANGIOSPERMS, GYMNASPERMS, PTERIDOPHYTA, BRYOPHYTA, ALGAE, PROTOPHYTA, LICHENS, FUNGI and BACTERIOLOGY) and the more important organs (see STEM, LEAF, ROOT, FLOWER, FRUIT); (*b*) Anatomy, the study of internal structure, including minute anatomy or histology (see PLANTS: *Anatomy*).

2. Cytology (*q.v.*), the intimate structure and behaviour of the cell and its contents—protoplasm, nucleus, etc.

3. Physiology, the study of the life-functions of the entire plant and its organs (see PLANTS: *Physiology*).

4. Systematic, the arrangement and classification of plants (see PLANTS: *Classification*, under which reference will also be found to various special articles).

5. Distribution or Geographical Botany, the distribution of plants on the earth's surface (see PLANTS: *Distribution and Ecology*).

6. Palaeontology, the study of the fossils found in the various strata of which the earth is composed (see PALAEOBOTANY).

7. Ecology, the study of plants in relation to each other and to their environment (see PLANTS: *Distribution and Ecology*).

8. Plant-pathology or Phytopathology, the study of the diseases to which plants are subject (see PLANTS: *Pathology*).

9. Genetics, including plant-breeding, the study of the facts and causes of heredity (see HEREDITY and PLANT-BREEDING).

Besides these departments which deal with botany there are various applications, such as forestry (see FORESTS AND FORESTRY), agriculture (*q.v.*), horticulture (*q.v.*) and materia medica (use in medicine; see the separate articles on each plant).

(A. B. R.)

**BIBLIOGRAPHY.**—For the history of botany see E. Winckler, *Geschichte der Botanik* (1854); J. von Sachs, *Geschichte der Botanik* (Munich, 1875); Eng. trans. *A History of Botany 1530–1860* (Oxford, 1890); J. R. Green, *A History of Botany 1860–1900* (1909); E. L. Greene, "Landmarks of Botanical History," *Smithsonian Mis. Coll.*, vol. liv. (1909); *A History of Botany in the United Kingdom* (1914); Ellison Hawks, *Pioneers of Plant Study* (1928).

For bibliographies on the main departments of botany mentioned in the section *Subdivisions*, see the various separate articles treating these subjects, as ALGAE, ANGIOSPERMS, BACTERIA, BRYOPHYTA, FUNGI, GYMNASPERMS, LICHENS, PLANTS, PROTOPHYTA, PTERIDOPHYTA, etc.

**PLANTS.** In the most generally used sense a plant is a member of the vegetable class of living things, plants and animals being the two classes into which living things (organisms) are roughly divided. With the higher forms the difference is very

definite and leaps to the eye. In the case of lower forms of life the distinction is often very difficult and indeed an artificial one, since plants and animals have had common ancestors in evolution. The early use of the word was for a twig, shoot, cutting or sapling. In the following sections the botanical sense of the term is followed. An outline of the classification of plants is given under BOTANY and the chief groups, Algae, Fungi, Gymnosperms, etc., are dealt with in separate articles.

## CLASSIFICATION OF PLANTS

In the article BOTANY reference has been made to the earlier systems of classification and the evolution of the idea of a natural system in which families are grouped according to their affinities. Details of classification *within* the large groups are given in the special articles on these groups. An outline of the generally accepted system of classification of the groups is given below.

Plants are usually divided into CRYPTOGAMS, in which there are no flowers producing seeds, the sexual reproductive organs being inconspicuous, and PHANEROGAMS, in which the plants bear flowers or flower-like structures from which seeds arise. The term SPERMOPHYTA is sometimes used for Phanerogams. To the more complex Cryptogams which show vascular strands (see PLANTS: *Anatomy*) the term Vascular Cryptogams is often applied.

**Cryptogams.**—The lower groups of Cryptogams are classified as THALLOPHYTA, *i.e.*, plants possessing a thallus or plant body which shows no differentiation into stem and leaves. The large groups of the Thallophyta are the PROTOPHYTA, the most primitive group; ALGAE, a group mostly of aquatic plants, showing coloured pigments (green, red, brown, etc.); BACILLARIALES or DIATOMS, a group of minute, brown plants sometimes classed with the Algae; and the FUNGI and BACTERIA, which are colourless parasitic or saprophytic plants probably derived by reduction from alga-like ancestors. To all these groups special articles are devoted, and also to the lichens, a peculiar group of composite plants, consisting of an alga and a fungus living in association.

The BRYOPHYTA (*q.v.*), which include the liverworts and the Musci or true mosses, are distinguished from the Thallophyta by the fact that the plant body often shows a distinction into stem and leaves, and the female reproductive organs are structures known as archegonia.

The group PTERIDOPHYTA, or fern-like plants, includes all the cryptogams higher than the Bryophyta. The plants often show a marked differentiation into leaves, some of these being of very great size and much divided. Furthermore they show well marked vascular strands (see p. 6) and their female reproductive organs are archegonia. This large group includes the Filicineae (true ferns), the Equisetineae (horsetails, etc.); the Lycopodineae (club mosses, etc.) and the Pteridospermae (a fossil group) which are described under PALAEOBOTANY.

**Phanerogams.**—To this group, which is sometimes termed SPERMOPHYTA (or *Spermatophyta*), all the higher plants belong. It includes the GYMNASPERMS, in which the seed is not enclosed in an ovary and the male and female reproductive organs are not found contained in a single flower, and the ANGIOSPERMS, in which the seed is not naked but enclosed in an ovary and the male and female reproductive organs (stamens and carpels) are usually associated in a single flower.

**Classification of Angiosperms.**—This very large group of plants falls into two classes, MONOCOTYLEDONS and DICOTYLEDONS. The first being characterized by an embryo with one cotyledon (seed-leaf), a stem which usually shows no secondary thickening, and flowers with parts in threes. The second shows an embryo with two cotyledons, a stem which exhibits secondary thickening, and flowers with parts in fours or fives. The classification of angiosperms which is now usually followed, is that of A. Engler, the monocotyledons and dicotyledons being divided into a number of classes termed orders (or cohorts or series), the name of each order usually terminating in *-ales*. Each order includes a number of *families* (formerly termed "natural orders") many of which are dealt with in special articles; the name of the family usually terminates in *-aceae*.



An outline of Engler's classification is given below, the orders (series) being printed in block type and the families in italics. For the 11 orders of Monocotyledons a synopsis of the chief characteristics is given. A selection of the more important families is made in the case of the orders which include a large number of families.

### MONOCOTYLEDONS

Order 1. **Pandanales**—(Marsh herbs or shrubs or trees with large narrow leaves and compound heads or spikes of flowers. Seeds rich in endosperm.) *Typhaceae*, *Pandanaceae*, *Sparganiaceae*.

Order 2. **Helobieae**—(Water or marsh plants with cyclic or hemicyclic flowers, often enclosed in a spathe. Embryo large with little or no endosperm.) *Potamogetonaceae*, *Najadaceae*, *Alismaceae*, *Butomaceae*.

Order 3. **Triuridales**—(Saprophytes with scaly leaves and small long-stalked flowers.) *Triuridaceae*.

Order 4. **Glumiflorae**—(Usually annual or perennial herbs with naked flowers covered by bracts. Ovary unilocular with one ovule.) *Graminaceae*, *Cyperaceae*.

Order 5. **Principes**—(Plants often trees, leaves of large size often fan-like or feather-like, male and female flowers usually in spikes enclosed in a spathe, ovary superior and fruit a berry or drupe with rich endosperm.) *Palmaceae*.

Order 6. **Synanthae**—(Often palm-like or climbers or large herbs with male and female flowers arranged alternately over the surface of a spike.) *Cyclanthaceae*.

Order 7. **Spathiflorae**—(Herbaceous or woody plants, sometimes climbing, flowers on a simple spike [spadix] more or less enclosed in a bract.) *Araceae*, *Lemnaceae*.

Order 8. **Farinosae**—(Herbaceous or sometimes grass-like in habit, flowers cyclic, hermaphrodite or unisexual, androecium often reduced, ovary usually orthotropous, endosperm mealy.) *Bromeliaceae*, *Commelinaceae*, *Pontederiaceae*.

Order 9. **Liliiflorae**—(Usually herbs, often with bulb, corm or rhizome, perianth petaloid or glume-like; ovary trilocular superior or inferior; fruit a capsule or berry; ovule anatropous; endosperm fleshy or oily.) *Juncaceae*, *Liliaceae*, *Amaryllidaceae*, *Dioscoreaceae*, *Iridaceae*.

Order 10. **Scitamineae**—(Tropical, large, perennial herbs often with sheathing leaves; flowers hermaphrodite and irregular, androecium often reduced; ovary inferior usually trilocular; fruit, a berry or capsule with numerous seeds with much perisperm, little or no endosperm.) *Musaceae*, *Zingiberaceae*, *Cannaceae*.

Order 11. **Microspermae**—(Flowers of a pentacyclic trimerous type but often with great reduction in the stamens; ovary inferior; fruit, a capsule with numerous minute seeds containing a very small undifferentiated embryo.) *Orchidaceae*, *Burnaniaceae*.

### DICOTYLEDONS

ARCHICHLAMYDEAE.—(Flowers often without a perianth, usually polypetalous; pollination entomophilous in the lower orders, anemophilous in the higher orders.)

Order 1. **Verticillatae**—*Casuarinaceae*.

Order 2. **Piperales**—*Piperaceae*, *Chloranthaceae*.

Order 3. **Salicales**—*Salicaceae*.

Order 4. **Garryales**—*Garryaceae*.

Order 5. **Myricales**—*Myricaceae*.

Order 6. **Balanopsidales**—*Balanopsidaceae*.

Order 7. **Leitneriales**—*Leitneriaceae*.

Order 8. **Juglandales**—*Juglandaceae*.

Order 9. **Batidales**—*Batidaceae*.

Order 10. **Julianiales**—*Julianiaceae*.

Order 11. **Fagales**—*Betulaceae*, *Fagaceae*.

Order 12. **Urticales**—*Ulmaceae*, *Moraceae*, *Urticaceae*.

Order 13. **Proteales**—*Proteaceae*.

Order 14. **Santalales**—*Santalaceae*, *Loranthaceae*, *Balanophoraceae*.

Order 15. **Aristolochiales**—*Aristolochiaceae*, *Rafflesiaceae*, *Hydnoraceae*.

Order 16. **Polygonales**—*Polygonaceae*.

Order 17. **Centrospermae**—*Chenopodiaceae*, *Amarantaceae*, *Phytolaccaceae*, *Caryophyllaceae*.

Order 18. **Ranales**—*Nymphaeaceae*, *Ranunculaceae*, *Berberidaceae*, *Magnoliaceae*, *Lauraceae*.

Order 19. **Rhoeadales**—*Papaveraceae*, *Cruciferae*, *Resedaceae*.

Order 20. **Sarraceniales**—*Sarraceniaceae*, *Nepenthaceae*, *Droseraceae*.

Order 21. **Rosales**—*Podostemaceae*, *Crassulaceae*, *Saxifragaceae*, *Hamamelidaceae*, *Platanaceae*, *Rosaceae*, *Leguminosae*.

Order 22. **Pandales**—*Pandaceae*.

Order 23. **Geraniales**—*Geraniaceae*, *Oxalidaceae*, *Tropaeolaceae*, *Linaceae*, *Rutaceae*, *Meliaceae*, *Polygalaceae*, *Euphorbiaceae*, *Callitrichaceae*.

Order 24. **Sapindales**—*Buxaceae*, *Empetraceae*, *Aceraceae*, *Sapindaceae*, *Balsaminaceae*.

Order 25. **Rhamnales**—*Rhamnaceae*, *Vitaceae*.

Order 26. **Malvales**—*Tiliaceae*, *Malvaceae*, *Sterculiaceae*.

Order 27. **Parietales**—*Dilleniaceae*, *Ochnaceae*, *Elatinaceae*, *Cistaceae*, *Bixaceae*, *Violaceae*, *Passifloraceae*, *Begoniaceae*.

Order 28. **Opuntiales**—*Cactaceae*.

Order 29. **Myrtiflorae**—*Thymelaceae*, *Elaeagnaceae*, *Lythraceae*, *Rhizophoraceae*, *Myrtaceae*, *Onagraceae*, *Hippuridaceae*.

Order 30. **Umbelliflorae**—*Araliaceae*, *Umbelliferae*, *Cornaceae*.

SYMPETALAE.—(Flowers usually sympetalous—with the parts of the corolla more or less united, often resulting in a tubular flower.)

Order 1. **Ericales**—*Pyrolaceae*, *Ericaceae*, *Epacridaceae*.

Order 2. **Primulales**—*Myrsinaceae*, *Primulaceae*.

Order 3. **Plumbaginales**—*Plumbaginaceae*.

Order 4. **Ebanales**—*Sapotaceae*, *Ebenaceae*.

Order 5. **Contortae**—*Oleaceae*, *Gentianaceae*, *Apocynaceae*, *Asclepiadaceae*.

Order 6. **Tubiflorae**—*Convolvulaceae*, *Polemoniaceae*, *Boraginaceae*, *Verbenaceae*, *Labiatae*, *Solanaceae*, *Scrophulariaceae*, *Bignoniaceae*, *Orobanchaceae*, *Acanthaceae*.

Order 7. **Plantaginales**—*Plantaginaceae*.

Order 8. **Rubiales**—*Rubiaceae*, *Caprifoliaceae*, *Adoxaceae*, *Valerianaceae*, *Dipsacaceae*.

Order 9. **Cucurbitales**—*Cucurbitaceae*.

Order 10. **Campanulatae**—*Campanulaceae*, *Compositae*.

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### MORPHOLOGY OF PLANTS

The morphology of plants consists in their comparative study from the point of view of *Form*. It treats not only of the external contour of the plant-body, *External Morphology*; but also of the internal contours of the constituent tissues, as revealed by anatomical study, the *Morphology of Tissues*. For the full understanding of form it does not suffice to examine the adult state only. It was found early that difficult questions of comparison could be illuminated by observation of development of the individual, that is, of its *Ontogeny*. This led to views based upon comparison as to the historical origin and descent of the parts compared, or even of the plant as a whole. A further step to the study of the parts as organs, carrying out certain distinct functions, gives the aspect now designated as *Organography*. These methods of enquiry are used collectively as a basis for evolutionary or sys-



tematic conclusions. But such conclusions are apt in critical cases to take the form of expressions of opinion which may differ widely. In arriving at a decision the most positive source of knowledge is the evidence of geological succession in time, and comparison of the forms constituting that succession. This is yielded by the study of fossil plants, called *Palaeophytology* or *Palaeobotany* (*q.v.*). But its record is so incomplete as to leave many problems unsolved. The morphology of plants thus conceived bears within it the possibility of reconstructing the evolutionary history of the vegetable kingdom, which is the goal to which all such study converges. This is called *Phylogeny*.

**Pre-evolutionary and Evolutionary Morphology.**—The aspect of morphology thus sketched is modern, dating in its present form from the period of the *Origin of Species*. But with varying success pioneer efforts had been made to found a science of plant-form before 1859, when Darwin's book was published. At first these related to the parts that constitute the plant-body as seen in the higher flowering plants. The foundation of organography was traced to Aristotle by Vines. More recently classification of members of the plant-body by Jung (1657), and observations on their ontogeny by Wolff (1759) resulted in a view summarized by the latter in these remarkable words: "In the entire plant whose parts we wonder at as being, at the first glance, so extraordinarily diverse, I finally perceive and recognize nothing beyond leaves and stem, for the root may be regarded as a stem. Consequently all parts of the plant, except the stem, are modified leaves." With such a conclusion already before him it was an easy step for Goethe (1790) to enunciate his theory of Metamorphosis of Plants: in particular he visualized an ideal leaf of the nature of a foliage leaf, of which the bracts and floral parts were held to be metamorphosed types.

The theory of evolution, long entertained before but galvanized into active existence by the genius of Darwin, revolutionized morphology (*Origin of Species*, 1859). For those whose vision was clear it converted it at a single stroke from a deductive handling of abstract ideas based chiefly on the higher plants, to an inductive argument rising, as Bacon said, successively from particulars to axioms of the lowest generality, then to intermediate axioms, and so to the highest.

This newer evolutionary or phyletic morphology, better designated as organography, starts with simple unicellular and aquatic organisms, such as the Flagellates. Each is a minute naked protoplast of inconstant form. A first step towards definite plant-organization is *encystment* within a firm cell-wall: this state appears as an incident in the life of many Flagellates, the encysted cell taking an approximately spherical form. Growth of such a green cell gives better opportunity for nutrition, and for storage of the material acquired: and an enlarging spherical form may be retained by organisms that float in the uniform medium of water. But the relation of an enlarging body to external conditions not uniform is liable to result in *polarity*, with the fundamental distinction of *apex* and *base*. The latter commonly attaches itself to any solid substratum, even without division of the single cell. But usually cell-division follows upon increasing size. If polarity be strongly marked, and growth continued, a filamentous plant-body may result, consisting of a chain of cells attached at its base. This may be further elaborated by cleavage of cells and by branching, while still attached at its base. In this we see initiated another leading characteristic of plant-organization, viz., *fixity of position*.

The sacrifice of mobility consequent on a fixed position is seen in all but the simplest plants: it accords well with the requirements of a self-nourishing green organism, but it imposes limits upon certain of the essential functions of competitive life. The nourishment of the plant must be brought to it by external agencies, such as diffusion, and absorbed from the medium, molecule by molecule. A raptorial habit, as in animals, is then unnecessary, and is even precluded by the fixed habit. On the other hand, the propagative cells must either themselves be motile or must be easily spread by external forces: otherwise any extension of field would be impossible. Throughout descent these two facts have dominated the morphological evolution of plants.

Since all nutrition is primarily a function of surface, the larger

the size of the organism and the more complicated its form, other things being equal, the better the nourishment of the individual, and the greater will be its propagative capacity. In simple organisms increase in size may be general throughout the plant-body. But in all larger plants *growth is localized*. Sometimes it is *intercalary* at some point between apex and base; but usually it is distal or apical. Where tissue-formation is thus localized the cells involved in it retain their youth as embryonic cells: this is especially marked at the distal tip, which has thus the character of a *growing point*, or *punctum vegetationis*. Here not only is provision made for continued growth of a central axis, but also for the initiation of successive branchings, which often mature as lateral appendages upon it. The result in the higher plants is the leafy shoot. These elaborations of the vegetative system may be seen illustrated either in the successive stages of an individual life, or by comparison of distinct organisms, such as a seaweed, a liverwort, a fern or a flowering plant. With varying detail these all share that distinctive feature of the more elaborated plant-body, its *continued embryology*. In all the higher animals the embryonic phase is a transient step towards full development, resulting in limbs definite in number and position: but plants have the power of forming an indefinite number of parts, in a succession theoretically without term or limit. Every bud of a forest tree or of a herb contains its own growing point deeply embedded among the successive leaves it has produced, and holds the potentiality of unlimited further development. *This continued embryology is the leading feature in the organization of the enlarging plant-body.*

**Categories of Parts.**—The vegetative system of the more highly organized plants consists of parts which have been classed as *stem*, *leaf*, *root*, *emergence* and *hair*. So long as the more highly organized plants alone are studied these categories appear fairly distinct. But when such comparison is applied to include forms lower in the scale, the less complete differentiation of their parts raises many questions touching the evolutionary origin of the several categories themselves. Here the fossil evidence takes its place: for conclusions based upon structure, position, individual development or comparison are liable to be checked by the discovery of some ancient form that may raise a doubt, or present even a firm negative. Thus the conception of a leaf as a lateral appendage upon a stem that is fixed at its base by roots, involves three categories of parts well marked in the higher vascular plants. How does this accord with the existence of the Devonian fossil *Hornea*, which is a vascular plant without leaves or roots? It is clear that those categories are not absolute, but are results of evolutionary history still incomplete in *Hornea*.

Many difficult questions as to the category of parts are apt to arise when we attempt their classification in plants at large. Mere comparison of external form or even of internal structure will not suffice: decisions must be based upon the origin and the place which the parts take relatively to other parts at the time when they first appear. Following this method, those parts of the individual, or of different individuals, species or genera, have been distinguished as *homologous* which bear the same relation to the whole plant-body, whatever their form or function or external conditions may be. On the other hand, parts may resemble one another in form and in function, though they may differ in their relation to the whole plant-body. Such parts have been described as *analogous* one with another. For instance, the flat green organs of the butcher's broom are by origin axillary buds, not leaves. Though their main function is like that of leaves, nutritional, they are only analogous to leaves.

*Homology* presents a more difficult problem, for in plants there may be various degrees of that closer correspondence of parts connoted by the term. The strictest conception of homology is that designated *homogeny*, which may be defined as including those structures which are genetically related in so far as they have a single representative in a common ancestor (Lankester). This implies repetition of an individual part bearing a definite relation to the whole organism. In plants with their continued embryology such correspondence is rarely possible, owing to the indefinite number of appendages produced. And yet the leaves of





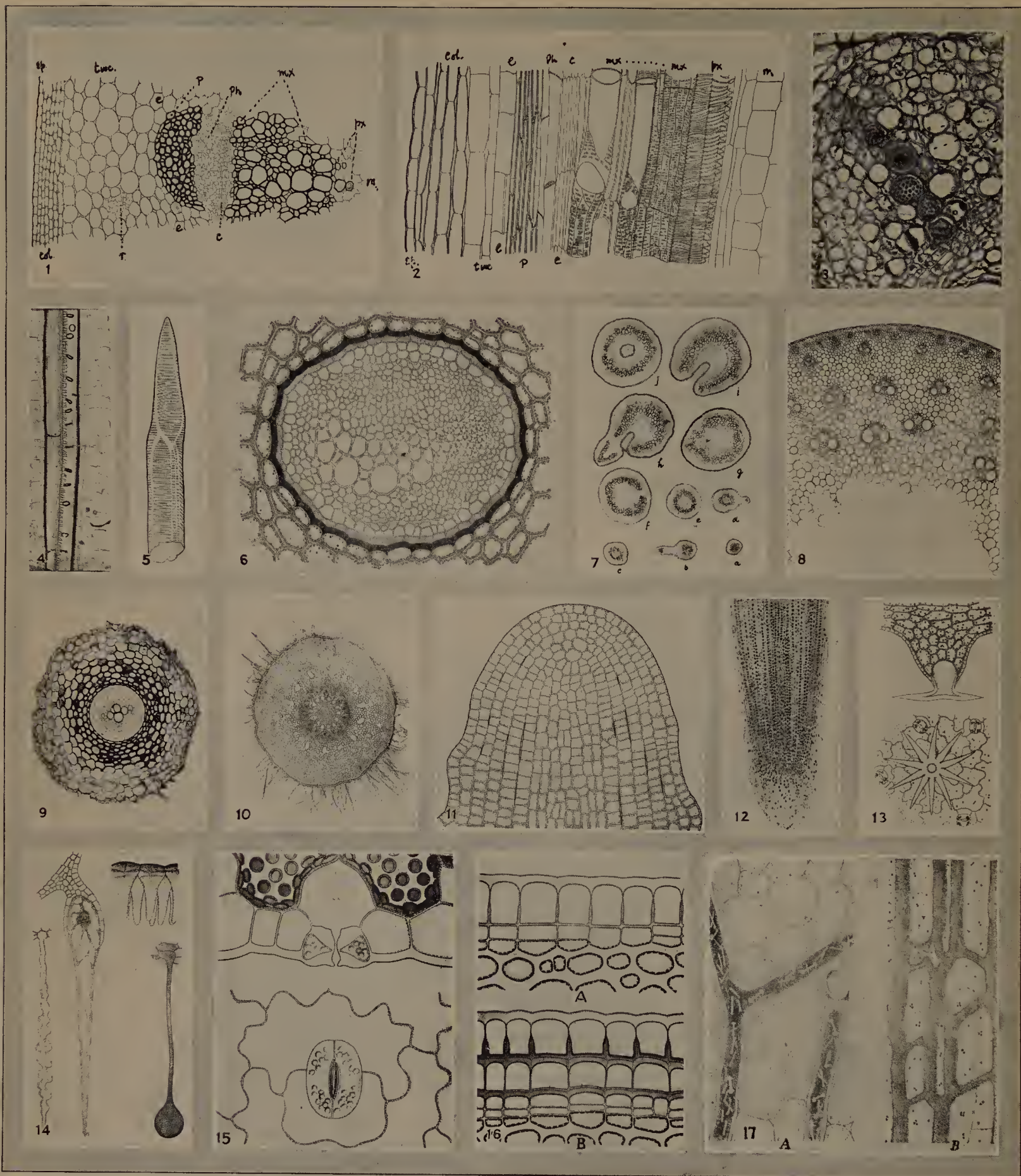
BY COURTESY OF (2-6, 10, 13) PAUL PAREY, FROM KNY, "BOTANISCHE WANDTAFELN"

### EXAMPLES OF THE DIFFERENTIATION OF PLANT CELLS

1. Group of individuals of the unicellular Green Alga (*Chroococcus*), one of which is in a state of division, as an example of an undifferentiated autonomous assimilating cell. (n.) nucleus; (chl.) chloroplasts; (pr.) cell protoplasm; (c.w.) cell-wall. 2. Plant of the primitive Siphonous Green Alga (*Botridium granulatum*). The cell sends colourless tublets (rhizoids, rh.) into the mud on which it grows. The upper part contains the chloroplast. 3. Portion of a plant of a multicellular Red Alga (*Lejolisia mediterranea*). The upper branches are reproductive, and a basal cell is expanded as a special holdfast (r.). 4. Portion of a fertile plant of the Liverwort (*Marchantia polymorpha*), with numerous rhizoids, lower surface. 5. Surface view of a breathing pore of *Marchantia polymorpha*. 6. Section of the upper layers of the body of a mature plant of *Marchantia polymorpha*. (b.p.) breathing pore. 7. Male plant of the Moss (*Funaria hygrometrica*), with basal rhizoids. 8. Transverse section of the aerial stem of the Moss (*Polytrichum commune*); (h) hydrom,

(l) leptom, (am) amylon, (st) sterom, (lt) leaftrace. 9. Transverse section of "leaf" of *Polytrichum commune*, showing photo-synthetic plates attached to upper surface on right. 10. Portion of a transverse section of a stem of the common Lime (*Tilia europea*), showing three annual rings and peripheral cork. 11. Plan of construction of a Lime stem after four years of secondary thickening. The medullary rays are represented by black lines in the radial and transverse views, and by black dots on the exposed tangential wood surface. 12. Twig of the Horse Chestnut (*Aesculus Hippocastanum*), with lenticels (lc). 13. Transverse section of a lenticel and subjacent cortex, from the stem of the Elder (*Sambucus nigra*). 14. A dorsiventral leaf. Portion of a transverse section of the leaf-blade of the Privet (*Ligustrum*), showing upper palisade and lower spongy tissue. 15. An isobilateral leaf. Portion of a transverse section of the leaf-blade of the Iris, showing a stoma of the lower surface (near centre, lower margin of picture), and no differentiation of palisade tissue





PHOTOGRAPHS, (6, 11, 13, 14, 15, 16, 17) AFTER KNY'S "BOTANISCHE WANDTAFELN" BY COURTESY OF PAUL PAREY

### ANATOMY OF VARIOUS PLANT STRUCTURES

1. Part of transverse section of the stem of Sunflower, ep. epidermis; col. collenchyma; tuc. thin-walled cortex; r. resin passage; e. endodermis; p. pericyclic fibres; ph. phloem; c. cambium; mx. metaxylem; m. medulla. px. protoxylem. 2. Radial longitudinal section, same stem. (Lettering as in fig. 1.) 3. Cross-section of phloem of stem of Cucurbit, showing four sieve plates. 4. Longitudinal section of the wood of a stem bundle of Maize plant, showing reticulately pitted, spiral and annular vessels. 5. Part of a Fern tracheid, with pointed end and scalariform pits. 6. Cross-section of a vascular bundle from the leaf-stalk of a Fern. 7. Sections of the stele of a Fern (*Loxosoma*), from the juvenile to the adult stem: (a) solid proto-stele; (b) medullated proto-stele; (c) and (d) medullated proto-stele with inner phloem; (e) and (f) widening of the phloem cylinder; (g) and (h) pocket of inner endodermis joined to outer endodermis at a leaf gap; (i) a transitional state to (j), which shows solenosteole of adult stem. 8. Cross-

section of stem of young Bamboo, showing scattered bundles. 9. Transverse section of the root of a Fern (*Pellaea*), with diarch xylem and sclerotic cortex. 10. Transverse section of the aerial root of *Vanilla*, with polyarch xylem and numerous root hairs. 11. Radial longitudinal section, stem apex of an Angiospermic plant. 12. Radial longitudinal section, tip of root of the Onion, showing root cap. 13. Surface and sectional views of a stellate hair of an Angiosperm. 14. Examples of forms of hairs of Angiosperms. 15. Sectional and surface views of a stoma from the leaf of an Angiosperm stem. 16. Stages in formation of cork and phelloderm as seen in cross-section of an Angiospermic stem: (A) the first division of the sub-epidermal phellogen; (Lower) the completion of a layer of cork. 17. (A) Part of a Laticiferous Cell from the stem of a *Euphorbia*, containing bone-shaped starch grains; (B) Laticiferous vessels in the root of an Angiosperm



a shoot are comparable in other respects; but their homology can only be recognized in a less stringent sense than homogeneity. Further, it may be held as doubtful whether all such parts as those designated "leaves" represent any essential plan of construction applicable to plants generally. The question arises whether leaf-like organs may not have originated independently in distinct phyletic lines: for instance, among the higher Algae, the Bryophytes, and the vascular plants. These diverse leaf-like organs may rather be regarded as being based upon such uniformity of results as has been achieved polyphyletically in descent, that is, by various types of organisms independently. In that case their likeness would be described as *homoplastic* (Lankester).

**Limiting Factors.**—Given a sufficient nutritive supply, continued growth of the plant-body may bring the organism up against certain limiting factors, of which the most obvious are concerned with mechanical stability, and the preservation of a due balance between surface and bulk, whether of the external contours, or of the internal tissue-surfaces. The *size-factor* may thus dominate not only the possible dimensions, but also the form of the plant-body and of its constituent tissues. The underlying principle is that of "similar structures," long ago recognized by Galileo, and familiar to architects and engineers. Applying it mechanically the strength of a structure varies as the square of the linear dimensions, and the mass or weight as the cube. Any plant endowed with continued growth, and with branching, is constantly approaching a size-limit defined by mass versus strength. Somewhat more than 300ft. is the extreme practicable height for a tree with the usual proportions and type of construction of the trunk, branches and twigs. A higher trunk would bend or break under the stress of wind.

The size-factor is also an effective influence on form; this is seen in respect of the proportion of surface to bulk. If the same form is maintained in an enlarging body, its surface increases as the square, while the bulk increases as the cube of the linear dimensions. Since nutrition and transit of materials are dependent upon surface action, the maintenance of a due proportion of surface to bulk in an enlarging organism may become critical. Its effect may be traced externally in the subdivision of submerged leaves, or indeed in foliar development itself: or it may appear internally in the complicated segregation of the vascular tracts in plants where cambium is absent or sluggish, as in the ferns or Lycopods. Such influences of the size-factor have long been recognized by animal morphologists: they are now beginning to find their place in the morphology of plants. (See F. O. Bower, *Proc. Roy. Soc. Edin.*, vol. xli., xliii.)

**Causal Morphology.**—The influence of the size-factor may be offered as an example of causal morphology, that is, the relation of form to environmental influence. It must suffice here merely to mention those better known branches of its experimental study which deal with the relation of form to such influences as gravity and light. Hofmeister introduced experiment in this field in his *Allgemeine Morphologie der Gewächse* (1868) as a corrective to the idealistic morphology of the previous period. His observations dealing with the arrangement and final form of the parts constituting the shoot were the natural precursors of the later work of Sachs, who recognized that the form and manner of life of plants "must in great part have arisen through the perpetual operation of gravity and light." (*Vorlesungen*, 2te Aufl: p. 545.)

**Adaptation.**—The scabiness or succulence of isolated species or genera under xerophytic conditions may be taken as examples of protective adaptation. Such characters are often hereditary: for instance, the succulence of a cactus or of a spurge appears in the seedling, even when grown in moist air: a seedling parasite, such as the dodder, produces parasitic seedlings that require attachment to the host for full development. Here the germ cell carries the character held as adaptive. On the other hand many formal characters that are specially related to climate or soil may be less marked, or even absent in the offspring grown under medium conditions. They have not been permanently stamped upon the germ-cells. Such differences raise the general question of the inheritance of adaptive form.

**Inheritance of Adaptive Characters.**—Direct experiments

that adaptive or impressed characters may be inherited in plants have so far given indecisive or negative results. All such experiments necessarily range within the narrow limits of laboratory time. If, however, a sequence of events conducted with the latitude of geological time gives a positive result, it seems right to give such a positive conclusion precedence over observations limited to a brief period. More than one good case has recently been brought forward showing the establishment of an ontogenetic adjustment as a permanently inherited character, where a consecutive evolutionary sequence of steps in its appearance can be traced from early geological periods, and confirmed by comparison of living species and genera. (See F. O. Bower, *Ferns*, vol. iii., Cambridge, 1928.) The conclusion follows that, in plants at least, direct ontogenetic adjustments, if repeatedly imposed, may become hereditary. Other opinions are held on this point, especially by zoologists (see LAMARCKISM, HEREDITY). If such inheritance were wide-spread or general, an important factor would be supplied in explanation of the prevalent phenomenon of adaptation.

But it would not provide a full explanation. The nature of the organism is the more decisive factor in adaptation. It suggests a tendency of initiative in the organism itself, which would go far to explain certain broad features in evolution. Intensive study of the coherent class of the ferns has shown similar trends of advance in distinct phyla-parallel changes which constitute together a positive phyletic drift. This may be held as determined by the "nature of the organism": and to it, acting on differences in that nature, may be attributed the results which we see worked out in those distinct classes and divisions of the vegetable kingdom, which nevertheless may have evolved under conditions essentially alike.

A frequent consequence of homoplastic adaptation is *convergent evolution*, with a high degree of similarity, or even of *standardization* as the final result. Examples of this are frequent in the vegetative system: for instance, in the phyllodes of *Acacia* and *Oxalis*, and the xerophytic leafage of *Veronica* and *Cupressus*: also in the prevalence of trimerous and pentamerous flowers. But it is in the propagative organs that it is most remarkable, leading to the high uniformity of the archegonia seen throughout the higher cryptogams, of the megaspores of the heterosporous types, and of the embryo-sacs in Angiosperms. Such standardization of parts, which can hardly have been in any of these examples strictly homogenetic, greatly increases the difficulty of their phylogenetic treatment, so far as it is based upon features apparently so similar.

**Alternation of Generations.**—A few examples must suffice in illustration of the working out of the principles thus underlying the more recent developments of plant-morphology. The first is the phenomenon of *Alternation of Generations*. In mosses and ferns the life-history comprises two distinct phases, or generations, which appear in alternate succession. In the ferns the one is the leafy *fern-plant*, which as it bears sporangia containing spores, is called the *sporophyte*: the other is a small green scale, the *prothallus*, which bears the sexual organs, or gametangia, containing the gametes, known as the spermatozoid, and ovum or egg: it is therefore called the *gametophyte*. These alternate generations together constitute a life-cycle of two somatic stages, each limited by a unicellular state, for each spore may germinate to form a prothallus, and each fertilized egg may grow into a new fern-plant (see PTERIDOPHYTES). Such a cycle exists in the life-history of all mosses and ferns, while its correlative stages appear also in modified form in seed-plants: moreover it is now proved that a like alternation exists also in many Algae and Fungi. *In fact an alternating cycle, with varying proportion of somatic development, underlies the morphology of all plants that possess sexuality.*

Strasburger (1897) related this cycle with the cytological state of the respective stages (see CYTOLOGY). Since in fertilization (*syngamy*) the number of chromosomes is doubled, the generation that springs from it is (2x) *diploid* (e.g., fern-plant, moss sporogonium): in the tetrad-division that precedes spore-formation, a corresponding reduction (*meiosis*) is effected, and the generation that springs from the spore is (x) *haploid* (e.g., fern-prothallus,



moss-plant). It is a morphological problem of the first rank to determine the evolutionary relation of these generations to one another, whether in the individual, the phylum, or in plants at large.

Whatever the historical origin of alternation may have been, certain features in its further development were probably as follows. The land-habit of the Archegoniatae appears to have encouraged or fixed a biological difference between the generations: the gametophyte is characteristically semi-aquatic, while sexuality which is its end depends upon external liquid water: the sporophyte is characteristically a land-living body, often rooted in the soil, while the dissemination of the spores depends normally on dry conditions. Thus the alternate generations of the Archegoniatae accord well with an amphibial life, one being distinctly sub-aerial, the other not fully freed from dependence on external water. But the tie of aquatic fertilization (zoidiogamic) is inconvenient for land-living organisms: hence it is no surprise to find that the higher flowering plants have broken loose from it, by adopting fertilization by a pollen-tube (siphonogamic). The gametophyte by successive steps of reduction loses its independence as a separate generation, while the sporophyte becomes dominant. This state may be held as the last essential step in the adaptation of plant-life to a land-habit.

A second illustration of the working out of the principles summarised above may be taken from the leaf. Of all the vegetative organs the leaf raises questions most open to debate. In the older morphology an ideal leaf was envisaged, and other types of leaf were regarded as modifications of it. But the duty of an evolutionist is to look not to an idea, but to the facts supplied by the lower organisms. They show that, whether in the gametophyte or the sporophyte, a leafless state preceded foliar development. Moreover both fossils and living plants suggest that all leaf-like appendages did not spring from a common source, but polyphyletically.

The effect of such considerations is to relax the old rigid conception of "the leaf" as a morphological constant. Biologically a leafy shoot appears as a favourable advance on a simpler organization, bringing with it an increasing proportion of absorptive surface to bulk. The existence of a demand for this is common to enlarging organisms, and the foliar development appears as a consequence in any or all such. The facts indicate an independent response in many distinct phyletic lines, with the result that the leaves so produced would not be all homogenetic, but probably in high degree homoplastic.

**Conclusions.**—From the preceding sketch of current plant-morphology it is seen to be founded on the theory of evolution, used as a working hypothesis. Observed facts are interpreted from the point of view of phyletic history, the argument leading towards the reconstitution of evolutionary history. The difference between the older idealistic and the newer inductive morphology has been well drawn by Sachs. He pointed out "that the former fits new facts into a scheme of old conceptions, the latter deduces new conceptions from new facts" (*History of Botany*, 1890). But morphologists are still bound by an idealistic evolution theory, for some preconceived type is in their minds. The remedy lies in a refusal to accept any conclusion from comparison as definitive, unless based upon consecutive data derived from actual organisms phyletically related one to another. The consequence of this would be a greatly increased recognition of polyphyletic sequences. But it is better to entertain a wide theory of polyphyletic evolution, with that apparent indefiniteness of conclusion that follows in its train, than to accept questionable doctrines that bring satisfaction only to uncritical minds.

Finally there remains the question of causality. The causes of development can best be unravelled and their relations to the environment established by experiment. On the other hand, experiment by itself cannot reconstruct history: for it is impossible to rearrange for purposes of experiment all the conditions exactly as they were in an earlier evolutionary period: and even if this were done, can it be assumed that the subjects of experiment will really be the same? Consequently there must always be a margin of uncertainty whether a reaction observed under experi-

ment to-day would be the exact reaction of a past age. Nevertheless there is a great future before experimental morphology: and though it cannot wholly unravel the history of form, this should still be approached experimentally as well as objectively.

Thus the way had already been prepared for Modern views, associated with "hormones," and their influence on individual development indicates from yet another angle how morphology is becoming ever more closely knit to physiology. It has been said that it deals with the stereotyped results of physiology. This is true in so far as it points towards the historical aspect of morphology, extending back as it does to the remotest fossil records: while physiology deals observationally with the reactions of the present time. But a better summing up of the relations of these two branches of biological science would be that morphology deals with all phenomena of form, including such as are not yet physiologically understood.

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## ANATOMY OF PLANTS

The term "Anatomy," originally employed in biological science to denote a description of the facts of structure revealed on cutting up an organism, whether with or without the aid of lenses for the purposes of magnification, is restricted in the present article, in accordance with a common modern use, to those facts of internal structure not concerned with the constitution of the individual cell or structural unit of the plant body.

An account of the anatomy of plants naturally begins with the cell which is the proximate unit of organic structure. The cell is essentially an individualized mass of protoplasm, of small dimensions, and containing a differentiated protoplasmic body, called a *nucleus*. Other protoplasmic bodies, known as plastids, and inanimate matter, mainly in solution or suspension, are present. But all cells which are permanent tissue-elements of the plant body possess, in addition, a more or less rigid limiting membrane or *cell-wall*, consisting primarily of cellulose or some allied substance excreted by the living cell-body and serving to connect the different cells of a tissue (*see below*). Upon the characters of constitution, thickness and sculpture of the cell-walls the qualities of a plant-tissue largely depend. The life of all the cells in a plant-body may be prolonged or a number of the cells may die and their protoplasm be removed. Thus a tissue may consist of living encysted units combined with an inanimate framework of cell-walls, enclosing in their cavities solely liquids and gases. In such cases the characters of the adult tissue largely depend on the proportion and distribution, the stature, form and contents of the living and dead units, and on the nature of their walls. It is customary in plant anatomy to speak of the cell-wall with its enclosed cavity as "the cell," and of the contained protoplasm or other substances as *cell-contents*.

In all but the simplest forms the plant-body is composed of a number of cells associated in more or less definite ways. In the higher or more complicated plants the cells come to differ greatly among themselves so that the adult body is composed of definite systems of units. Each system has its own characteristic structure, depending partly on the characters of the component cells and partly on the method of association. Such a system is called a *tissue-system*, the word tissue being employed for any collection of cells with common developmental, functional or structural characters to which it may be conveniently applied, and accepted by the general resemblance which was thought to exist between the texture of plant-substance and that of a textile fabric before the fundamental constitution of plant-substance was discovered.

It is convenient here to define the two chief types of cell-form which characterize the tissues of the higher plants. The term *parenchyma* is applied to tissues the cells of which are isodiametric or cylindrical in form. The term *prosenchyma* is applied to tissues consisting of long narrow cells with pointed ends.

The reader is referred to special articles on the anatomy of the



lower plants (Thallophyta: Algae and Fungi, and Bryophytes: mosses and liverworts) in which the differentiation of tissues is comparatively slight. It must suffice here to mention that both Algae and Fungi range from the simplest unicellular forms with no external differentiation of the body to forms of greater stature and complexity of organization. The progress in complexity is closely associated with division of physiological labour among the component cells and with the adaptation of the multicellular organism to the needs of its environment. But whatever are the various states attained by individual genera the majority of the cells of the adult bodies of both Algae and Fungi remain alive and the tissues are essentially parenchymatous.

In accordance with the greater complexity in the conditions of life on land for self-supporting plants, considerably more advanced tissue-differentiation is exhibited by the Bryophyta, which are mainly terrestrial plants. In a general way this greater complexity consists (1) in the restriction of regular absorption of water to those parts of the plant-body which are in close contact with the soil, and (2) in the more regular evaporation of water from the parts exposed to the air. It is, however, in the higher vascular plants that those two principles find their fuller expression, for in the bryophytes water is still absorbed, as, for example, from rain or dew, by the general plant-surface. The lowest liverworts have an extremely simple vegetative structure comparable to that of many of the simpler Algae, for as their bodies are small and normally live in damp air the demands of terrestrial life on them are at a minimum. Thus their bodies consist of true parenchyma, and the vast majority of the component cells remain alive. Rooting and absorbing thread-like cells (*rhizoids*) universally occur on their lower surfaces in contact with the soil, and considerable tissue-differentiation may occur within the body. Thus some possess a distinct assimilative system consisting of branched chains of thin-walled cells packed with green plastids (*chloroplasts*) and arising from the bases of large cavities directed towards their upper illuminated surfaces. These cavities are completely roofed by a layer of surface cells pierced by pores, surrounded by special cells, and through which aeration and evaporation are freely maintained. In certain forms in which the body consists of thick midribs and delicate lateral leaf-like appendages strands or bundles of long thick-walled fibre-like (*prosenchymatous*) cells with pointed ends run longitudinally through the midribs, which are devoid of special assimilative tissue. The walls of these cells are strongly lignified (*i.e.*, consist of woody substance) and are irregularly thick and thin so as to be closely studded by simple pits which are usually arranged in spirals running round the cells and often elongated in the direction of the spiral. There is much variety of detail in the differentiation of the tissues of the liverworts, but the general plan of construction resembles that adopted in the leaves of higher plants.

In the mosses the plant-body is generally more elaborate in accordance with its fuller commitment to terrestrial life. There is always a radially organized supporting and conducting axis (stem) bearing laterally throughout the greater part of its length thin, flat assimilating and transpiring appendages (leaves). To the base of the stem or to those parts in contact with the soil are attached branched rhizoids. In some cases the stem possesses a special surface or epidermal layer of cells, but usually all the outer layers of the stem are composed of brown, thick-walled, lignified, prosenchymatous, fibre-like cells forming a peripheral *stereom* (mechanical and supporting tissue) which forms the *outer cortex*. This passes gradually into the thinner-walled parenchyma of the *inner cortex*. The entire cortex is generally alive and its cells often contain reserve foods in the form of starch. The centre of the stem, in the forms which live on soil, is composed of a strand of narrow, elongated, thin-walled, unlignified, dead water-conducting cells (*hydroids*) which are seldom pitted. This hydrom strand has in most cases no connection with the leaves, but runs straight up the stem and spreads out locally below the reproductive organs. In the aquatic and semi-aquatic forms, and in those mosses which live under conditions of extreme drought the entire plant-surface absorbs water, perpetually in the first two cases, and during rain in the third. In such forms the hydrom

strand is either slightly developed or altogether absent. The leaves of most mosses are flat plates, each consisting of a single layer of square or oblong assimilating cells containing chloroplasts. The marginal cells of the plates are frequently produced as teeth and their walls are thick. The centre of the leaf is often occupied by a midrib consisting of several layers of parenchymatous cells elongated in the direction of the long axis of the leaf and poor in chloroplasts. This midrib may be considered a primitive conducting foliar strand or *leaf-bundle*. Associated with this conducting parenchyma are frequently found hydroids like those of the central strand of the stem, and in some cases continued into the cortex of the stem as a *leaf-trace bundle* (the anatomically demonstrable *trace* of the leaf in the stem). In several cases the leaf-trace runs vertically downwards for some distance in the outer cortex and ends blindly in a fan-shaped expansion: in others it joins the central hydrom strand so that a connected water-conducting system is established between stem and leaf.

Further differentiation of tissues characterizes the highest family of mosses, the Polytrichaceae. In these elongated, living, nucleated cells with a thin lining of protoplasm surround the dead hydrom, and form the *leptom*, inferred to serve for the conduction of organic substances, since the entire cavity of a leptom cell is sometimes occupied by proteid contents. The ends of each leptom cell are slightly swollen and fit to the similar swollen ends of the next leptoids in a row. The end walls are usually very thin, and the protoplasm, on artificial contraction, commonly sticks to them though no perforations of the walls have been found. It is considered that these cells are in some measure comparable to the *sieve-tubes* of higher plants (*see below*). Associated with the leptoids are similar cells without swollen ends and with thick end walls, while between the hydrom and leptom is a cylinder of cell-layers, known as *amylon*, which may serve for the temporary reservation and in the distribution of carbohydrates, since they sometimes contain an abundance of starch. The underground portion of the stem (*rhizome*) bears rhizoids and simple scales. The aerial parts bear leaves, each with a simple midrib several cells thick with a strong band of stereom above and below a bundle of leptom, hydrom and amylon cells which join the central cylinder of the stem. Each midrib bears two wings, one cell thick, while above the midrib is a series of closely set, vertical, longitudinally-running plates of green assimilative cells.

**Vascular Plants.**—It is, however, in the higher vascular plants (Pteridophyta, *e.g.*, ferns, horse-tails, club-mosses and Phanerogama or flowering plants) that the greatest anatomical complexity is found, for these are the dominant land plants. Such plants are not exactly comparable with the bryophytes for while the body of the latter bears the sexual organs and is called a *gametophyte*, and later nourishes a simple spore-bearing body (*sporophyte*), the vascular plant is a sporophyte which later nourishes a simple and reduced gametophyte. Nevertheless the gametophytic bryophyte and the sporophytic vascular plant have similar physiological needs and are both fixed to the soil. The chief new feature in external conformation of the body of a vascular plant compared with that of a bryophyte is the presence of "true" roots, the first formed of which is a downward prolongation of the primary axis of the plant. From this and from various parts of the shoot-system other roots originate. The roots of Pteridophytes are structurally simple and uniform compared with those of Phanerogams, but all manifest a primary plan of construction in direct relation to their normally subterranean life and fixative and absorptive functions; they differ from aerial stems in the characters of their surface tissues, in the absence of the green assimilative pigment chlorophyll, in the arrangement of their vascular systems, and in their mode of apical growth. Great variety in stem- and leaf-form and structure is shown by the vascular plants.

But in spite of the many considerable differences of detail between Pteridophytes and Phanerogams, we can trace, alike in root, stem and leaf a threefold division of tissue systems, already indicated among the bryophytes, and expressive of the fundamental conditions of evolution of the bulky body of a land plant. Thus there is (1) a specialization of a surface layer of cells which regulates the immediate relations of the plant with its surround-



ings, while varying in expression in the subterranean and aerial parts. In the former the surface layer is pre-eminently absorptive and in the latter protective provision at the same time being made for the gaseous interchange of oxygen and carbon dioxide involved in respiration, and for such vital functions as assimilation and transpiration. This surface layer is known as the *epidermis*. On the other hand we have (2) an internal differentiation of conductive tissue, prefigured in the bryophytes, and collectively known in the vascular plants as the *vascular system*. The remaining tissue of the plant-body, which shows varied local differentiation and is concerned with special functions, is known by reason of its peripheral position in relation to the central conductive tissue as (3) the *cortex*. But besides absorption, assimilation, conduction and protection, provision is made for *support* and the *storage of food*. Thus locally in the cortex and vascular system special supporting tissues (*stereom*) may be developed according to the varied needs and the conditions of body-differentiation, and living cells of both the cortex and the vascular system may serve for temporary storage of foods and are specialized accordingly. The functions of aeration, assimilation and transpiration, by which the bulky tissues of the plant-body obtain oxygen for breathing and carbon dioxide for food-manufacture, and the removal of excess water is assured, are maintained by an extensive system of *intercellular spaces* communicating with the external air.

**Epidermis.**—The epidermis of the subaerial stems and leaves is primarily protective and usually consists of a single layer of living cells devoid of chloroplasts, and with thickened and cuticularized outer walls, defensive to slight shock and small parasites, but permitting controlled evaporation. At intervals it is interrupted by small pores (*stomata*) leading from the outer air to the system of cortical intercellular spaces, and serving for gaseous interchange between the primary tissues and the outer air. Each stoma is surrounded by a pair of peculiarly modified epidermal cells called *guard cells* which possess chlorophyll and open and close the pore, especially in accordance with the conditions of transpiration. The stomata of leaves are often situated at the bottom of pits in the leaf-surface. Thus transpiration is checked by the creation of a still atmosphere in the pit above the pore. Such an arrangement of the stomata is found especially in plants which require to economize their water supply if transpiration is in excess of absorption. In many plants living in conditions which tend to promote excessive transpiration at certain hours of the day, the epidermis is doubled or trebled and forms a *water tissue* which supplies the immediate needs of transpiration, and prevents the injury which would result in the epidermis if its cells were excessively depleted.

**Hairs and Scales.**—The epidermis of many species of vascular plants bears hairs or scales of varied form and function. Hairs are characteristic of stems and leaves of primitive pteridophytes and of many flowering plants, while scales characterize such pteridophytes as the advanced ferns. The simplest hairs consist of single elongated cells projecting above the general surface of the epidermis, while others consist of simple or branched cell-chains. The more complex scales are flat plates of cells commonly inserted on mounds or stalks, and may be placed parallel to the leaf-surface or projecting directly from it. By such emergencies transpiration is diminished by the stillness of the atmosphere between them. In other instances the hairs are glandular and excrete ethereal oils which tend to reduce transpiration, or they may be stinging, as in the common stinging nettle, in which the top of the hair is brittle, and when broken penetrates the skin and injects formic acid into the slight wound thus formed. In many cases both hairs and scales are shed before the stems and leaves are mature: in others they are retained throughout the life of the plant.

**Hydathodes.**—In many vascular plants special epidermal organs, known as *hydathodes*, are developed, especially on foliage leaves, and serve for the excretion of water in liquid form when transpiration is diminished so that the pressure in the water-channels of the plant has come to exceed a certain limit. Hydathodes are widely distributed in plants in certain tropical climates under which active root-absorption continues while the air is nearly

saturated with water-vapour. In some cases the hydathodes are specially modified single epidermal cells or are multicellular hairs without direct connection with the vascular system. The cells concerned, like all excreting organs, have abundant protoplasm and large nuclei, and in many cases part of the cell-wall is perforated and resembles a filter. In others the hydathodes are associated with the ends of conductive strands and consist of groups of richly protoplasmic cells, as in the leaves of many ferns, while in flowering plants the hydathodes are most commonly directly connected with subjacent water-collecting cells known as *epithem* which act as intermediaries for the hydathodes and conductive strands. To illustrate, water expelled through hydathodes is often observable on the tips of grass leaves on a summer's evening and is commonly confounded with dew. Its expulsion as droplets is, however, due to the more rapid cooling of the air than of the soil as night approaches. Thus while active absorption continues by the roots, transpiration by the leaves is reduced in the evening and the conductive strands are overcharged with water which is expelled by the hydathodes. There are many other types of glands such as *nectaries*, *digestive-glands*, *resin-* and *mucilage-glands*, serving the most varied purposes in plant-life. Some involve epidermal cells, while others are more deeply seated, but as they are not involved in the primary activities of the epidermis they are here passed over. It will, however, be apparent that the epidermis of the stem and leaf of a vascular plant may be highly specialized.

**Epidermis of Root.**—The epidermis of the root is fundamentally different from that of the stem or the leaf. In relation to its normal function of water-absorption its cell-walls are not cuticularized and usually remain thin. The absorbing surface is increased by many of the cells being produced into tortuous, delicate, unicellular tubes (*root-hairs*) which aid in anchoring the root, and readily absorb the surface films of water from the soil particles. A root-hair thus corresponds in function with a rhizoid of a bryophyte. The hairs are normally definitely restricted to a more or less definite zone of the root a little removed from the growing *root-tip*. At the lower limit of this zone hairs are constantly being formed as the root advances in the soil, while at the upper limit they have passed maturity, are dying and are being destroyed. Thus beyond the zone which at any moment bears living absorbing hairs (the *piliferous zone*) the epidermis is extensively or completely destroyed, and its place is taken by the immediately subjacent cortical layer, which is not absorptive, but becomes protective like the epidermis of the stem or leaf. At the apex of the root, covering and protecting the delicate tissue of the growing point, is a special *root-cap*, consisting of a number of layers of cells produced by continual active local division of the apical epidermal cells, and which break down into mucilaginous products towards the outer surface of the cap, thus facilitating the passage of the apex as it pushes between the soil particles, and keeping the apex continually moist.

**The Cortex.**—The cortex consists primarily of living parenchyma, but its differentiation may be extremely varied, and in the complex bodies of vascular plants its functions are varied and may be modified. The cortex of a young stem is usually green as its cells possess chloroplasts, and a fine system of intercellular spaces communicates with the external air through stomata. With age the inner cortical layers may lose their chlorophyll and become storage tissue, and the outer layers may be extensively modified (*see p. 10, secondary tissues*). In many pteridophytes (*e.g.*, ferns) the mature outer cortical layers of the stem and root are hard *sclerenchyma* with thick brown walls, but in flowering plants, while the stems are still slender, the cells of the outer cortical layers elongate and become cylindrical so that their intercellular spaces are widened. Vertical bands of cellulose thicken those regions of the walls which are in contact with the intercellular spaces, but the remaining regions of the walls usually remain thin. Such a tissue is known as *collenchyma*. It provides peripheral support for the growing stem, and as its cells are alive, is open to later modifications with changing needs in stems which undergo annual increase in girth. The wonderful recovery, after bending and stretching, which is often observable



in herbaceous stems, is in large measure due to the effective distribution of this elastic collenchyma. On the other hand sclerenchyma is commonly dead and provides a more rigid but usually unmodifiable supporting tissue. Its adequacy will be evident for stems such as those of modern ferns which do not increase annually in girth. Less commonly, scattered cells or cell-groups which increase little in length may become *stone cells*, with irregularly but inordinately thickened hard walls, while in some cases longitudinal rows of cells disintegrate thus forming canals, such as *resin canals*, the cortical wall-cells of which are excretory. Many such minor modifications of the original cortex of the stem occur in association with special localized functions.

**Phloeotherma.**—The innermost layer of the living cortex investing the central cylinder of the stem is, however, often early and peculiarly modified as a continuous cylinder called the *phloeotherma*. Throughout its entire course its cell-walls remain in close contact so that the system of intercellular spaces in the cortex is not continued into the central cylinder of conductive tissue. Towards the upper limit of the phloeothermal cylinder, while the stem is still young, the component cells may be rich in plastids in which starch grains are formed. In some localities the phloeotherma is known as a *starch sheath*, which is variously thought to play some rôle in the controlled conduction of carbohydrates from the assimilatory cortical cells to the vascular cylinder, or in some connection with the directional growth of the young stem. In the more mature regions of the stem starch grains are absent from the phloeothermal cells, the walls of which are somewhat thickened. In particular, a band of the lateral longitudinal and of the end walls is modified, being impregnated with a fatty substance which is thought to prevent radial transfer of foods in solution athwart the phloeotherma save under protoplasmic control of its cells. The phloeotherma is here known as an *endodermis*, and is thought to serve as a physiological barrier between the cortex and the central conductive cylinder.

**Mesophyll.**—The cortex of the leaf is primarily concerned with the primitive fundamental function of carbon assimilation, and to the active performance of this function the maximum exposure of living parenchymatous tissue containing chloroplasts is necessary. Thus the cortex of the leaf is essentially a green expanse of thin-walled parenchyma, known as the *mesophyll*, and is penetrated by a large and elaborate system of intercellular spaces which serve at one and the same time for the promotion of transpiration and respiration. The pathways for the gases which thus pass between the mesophyll and the outer air are the stomata, which in land plants with dorsiventral leaves are mainly or exclusively placed on the lower leaf-surface. By this means over-transpiration tends to be avoided, since the liberated water-vapour, being lighter than air, tends to remain in contact with the lower leaf-surface and checks evaporation. The stomata are in direct communication with the ample system of intercellular spaces in the mesophyll, the lower layers of which are commonly loosely arranged as *spongy tissue* with extensive intercellular spaces. This is the main transpiring tissue of the leaf, and in it chloroplasts may be comparatively few. It is protected from direct illumination and is at the same time liable to over-evaporation. The main assimilating tissue, on the other hand, is under the upper epidermis, is well illuminated, its cells are densely packed with chloroplasts, and are commonly oblong with their long axes perpendicular to the leaf-surface. The intercellular spaces are here narrow as between sticks in a bundle, and are in open communication with the spaces in the spongy tissue below. By reason of its resemblance to the boards in a fence, when viewed in a transverse section of the leaf, this portion of the mesophyll is called the *palisade tissue*. Leaves with blades held in a vertical position commonly possess palisade tissue on both sides or have little or no distinction in the form and arrangement of the cells of the mesophyll, since there is no difference in the illumination or other external conditions, while cylindrical or approximately cylindrical leaves may have palisade tissue all round. The leaves of shade plants have little or no differentiation of the palisade tissue. In fleshy leaves, which contain a great bulk of tissue in relation to their chlorophyll content,

the central mesophyll contains little or no chlorophyll and may consist of water-storage tissue, while locally a layer or mass of sub-epidermal cells may be thick-walled and fibrous.

The cortex of the leaf-stalk is transitional in structure to that of the stem and leaf-blade. The leaf-stalk is traversed by one or more vascular strands connected below to the central conductive system of the stem, and leading forward in the leaf-blade to a complex system of minor strands which ramify the mesophyll and run their course in the plane of junction of the spongy and palisade tissue. The layer of mesophyll immediately investing each bundle is *phloeotherma* and usually takes the form of a special parenchymatous sheath of elongated cells, distinguished otherwise from the rest of the mesophyll only by their poverty in chloroplasts. In a few rare cases the phloeothermal cells are rich in chlorophyll. These *bundle-sheaths* are considered important in the conduction of carbohydrates from the assimilative cells to the conductive strands and in the supply of water from the latter for transpiration. Their function is thus considered in some measure comparable with that of the phloeotherma of the stem.

The cortex of the roots of Pteridophytes is commonly extensively sclerotic at maturity, but in flowering plants the root-cortex generally remains a living parenchymatous food-storing tissue. Its innermost layer is invariably an endodermis.

### VASCULAR SYSTEM

Among the most striking characters of Pteridophytes and Phanerogams is the possession of a double (hydrom-leptom) conducting system, such as has been noted in the higher mosses, but with more sharply defined and specialized features. This is the *vascular system*, and associated with it are other tissues consisting of parenchyma and special stereom. The whole tissue-system is known as the *stelar system* (from the way in which in its simpler forms it runs through the whole axis of the plant as a column). When it is remembered that the moss plant is a gametophyte while the vascular plant is a sporophyte it will be realized that the vascular system of the latter is not the result of elaboration of the conductive system of the former, but that these vascular systems are most readily interpreted as somewhat similar products of differentiation in plants fitted for life on land.

**Tissue Elements.**—The hydroid of a Pteridophyte (e.g., a fern) is initially a living undifferentiated parenchymatous cell. As it dies it usually elongates and its wall is irregularly thickened and becomes woody (lignified). Its contents at maturity are watery solutions and air. The thickenings are on the inner wall-surface, are insufficient to line the wall entirely, and take the form of a spiral or complex network. The mature hydroid is called a *tracheid*. Its end walls persist and are commonly oblique. When the walls are mainly thickened their unthickened portions are called *pits*, and according to the varied distribution of the thickenings, the size, form, number and distribution of the pits depend. Thus in *spiral tracheids* a broad spiral band of unthickened wall persists, while when the thickenings on a wall-face are more or less transverse bars (often joined by short vertical bars) there is a resemblance to the rungs of a ladder, and we have a *scalariform tracheid*. All manner of transitions from spiral to scalariform tracheids may be found in a single plant. Spiral thickening is, however, characteristic of tracheids in which lignification begins and is completed while elongation of the cell is still in progress. Scalariform thickening is typical of tracheids which mature late or slowly, so that thickening may be continued after elongation is completed. The pits of scalariform tracheids are typically *bordered pits*, as the bars of thickening last deposited are widest. The pits on tracheid-walls which are in contact with each other are at similar levels so that at regular intervals the cavities of contiguous tracheids are only separated by a common thin area of wall (the *pit-membrane*). Sooner or later the pit-membrane disappears so that the mature tracheids come to consist of a framework of lignified bars with numerous small open communications between the cell cavities. Collectively with associated parenchyma the tracheids constitute the *xylem* or *wood*.

The leptoid of a Pteridophyte is also an elongated cell. It, however, remains alive, its wall is unlignified, it has a thin lining



of protoplasm, but is destitute of a nucleus. It is always in communication with its neighbouring cells in a leptom strand by exceedingly minute wall perforations through which protoplasmic continuity is maintained. It is generally supposed that through these perforations organic substances are passed from cell to cell as through a sieve. The cells are accordingly called *sieve-tubes*, and collectively with associated parenchyma constitute the tissue called the *phloem*, or *bast*. The phloem is typically distributed at the periphery of the xylem when the latter is massed centrally, but may occur in other positions (*see below*). Between the phloem and the phloeo-therma is a mantle of one or more layers of parenchyma forming the pericycle.

**Arrangement of the Vascular System.**—In vascular plants the xylem and phloem are nearly always found in close association in strands or *bundles*, but as is to be expected in so complex and varied a group as the Pteridophytes the arrangement of such bundles is by no means stereotyped either in the group or in the different parts or members of the plant-body. A connected vascular system runs, however, through the entire body. In the roots and leaf-blades the vascular system is comparatively simple. In the former a solid, slender xylem core is virtually invested by phloem, with a single layer of pericycle as a mantle in direct contact with a continuous cylindrical endodermis, beyond which is the bulky and often sclerotic cortex. The arrangement is thus virtually radial. The bundles in the leaf-blade are on a somewhat similar plane of simplicity, but their phloem is directed downwards, their xylem upwards, the tracheids are dominantly spirally thickened, and the phloem is scanty or entirely absent towards the slender bundle-endings. Similarly throughout the entire length of stem there may be a solid xylem core, surrounded successively by phloem, pericycle and endodermis. Such a vascular system is a *solid protostele*. The slender stems of most juvenile Pteridophytes are protostelic and despite widening of the *stele* in the more bulky portions of the adult plant, this primitive protostelic state may be maintained throughout the entire stem. In many cases, however, as in advanced ferns, the vascular system of the juvenile stem alone is a solid protostele. When followed upwards the core of the xylem strand may remain entirely parenchymatous. This parenchymatous core is the *medulla* or *pith*, and the stele is here called a *medullated protostele*. At higher levels the stem may show a different vascular arrangement, sieve tubes being differentiated in the centre of the medulla, at first as a solid strand, but later or higher as a cylinder with parenchymatous pith at its core and parenchyma between it and the xylem. At a still higher level there may be an inner endodermis between the pith and the inner phloem so that the succession of tissues from within as viewed in a transverse section of the stem may be medulla, inner endodermis, parenchyma (or inner pericycle), inner phloem, parenchyma, xylem, parenchyma, outer phloem, outer pericycle and outer endodermis. Such a local arrangement of the stelar elements is said to be *siphonostelic*, is considered an evolutionary advance on the protostelic state, and may characterize the entire upper portion of the adult stem.

When the vascular system is entirely protostelic the decurrent bundles from the leaves join the vascular system of the stem without disturbing the continuity of the latter. Thus throughout the entire plant the endodermis is an unbroken mantle. But in the siphonostelic portions of the vascular system of the stem, the pith and cortex are commonly in open parenchymatous connection through *gaps* in the stele, and round the edges of these gaps the inner and outer endodermal cylinders are united by endodermal cells. Thus here again the endodermis is a continuous tissue, and isolates completely the pith and the cortex from the vascular tissues. The gaps which occur immediately above the level of insertion of the leaf-trace bundles on the stele of the stem are called *foliar gaps*, while those which occur elsewhere are called *perforations*. When there is no overlapping of leaf-gaps the siphonostele is said to be *solenostelic*; when two or more leaf-gaps overlap, the stele is *dictyostelic*. Thus locally the vascular system of a Pteridophytic stem may be solenostelic or dictyostelic: likewise it may be locally a *perforated solenostele* or a *perforated dictyostele*. Rarely among ferns is there more

than a single vascular cylinder. The condition is described as *polycyclic*, and an outer and inner cylinder may be even united by oblique lateral strands. In such cases the leaf-trace strands are joined to the outer cylinder, while the inner cylinder may best be considered concerned with internal conduction.

**Structure of the Stele in Seed-plants.**—The typical structure of the vascular cylinder of the adult primary stem of the Gymnosperms (firs and their allies) and Dicotyledons (the dominant group of higher flowering plants)—all of which are seed-bearing plants—is, like that of the higher ferns, a hollow cylinder of vascular tissue enclosing a central parenchymatous pith. But unlike the ferns the seed-plants have no internal phloem (except as a special development in certain families) and there is no internal endodermis. The xylem and phloem rarely form perfectly continuous layers as in the solenostelic ferns, for the vascular tissue is typically separated into distinct *collateral bundles*, the xylem of which is usually wedge-shaped in cross section with the first formed xylem (*protoxylem*) at the inner extremity, while the phloem forms a band on the outer side of the xylem, and is separated from the latter by a band of conjunctive tissue (*mesoderm*). These collateral bundles are separated from one another by bands of conjunctive tissue called *primary medullary rays*, which may be quite narrow or of considerable breadth.

When the pith is large-celled, the xylem of the bundles is often separated from it by a distinct layer of conjunctive tissue called the endocycle, and a similar layer, the *pericycle*, separates the phloem from the cortex. The inner layer of the cortex (phloeo-therma) may form a well-marked *endodermis*, or may differ in other ways from the rest of the cortex. The pericycle, medullary rays, endocycle and mesoderm all form part of one tissue-system, the *external conjunctive*. The external conjunctive is usually a living and comparatively small-celled tissue, the cells of which are greatly elongated in the direction of the stem-axis and may be collenchymatous, sclerenchymatous, fibrous or food-storing. The conjunctive tissue of the stem is open to *secondary changes*, bound up with the thickening of the stem as it grows old. Most of the collateral bundles are leaf-trace bundles, *i.e.*, they can be traced upwards from any given point till they pass out of the cylinder, travel through the cortex of the stem, and enter the leaves. The remaining bundles (*compensation bundles*) which go to make up the cylinder, are united at some level with the leaf-trace bundles, and in turn form the traces of leaves at some higher level. Purely cauline vascular strands (*i.e.*, confined to the stem) are rare in the flowering plants, though common in Pteridophytes. The leaf-trace of any given leaf rarely consists of a single bundle only, the number of bundles in a trace is generally odd, and the median bundles of the trace are typically the largest.

*Foliar- or leaf-gaps* are formed in essentially the same way as in the ferns, but as the distribution of the bundles of a single trace may be wide and long, there may be a number of gaps in the cylinder associated with the insertion of the bundles of a single leaf-trace. The gaps are, however, often filled as they are formed by the development of external conjunctive tissue immediately above the points at which the bundles begin to bend out of the stele, so that sharply defined open gaps, such as occur in fern steles, are but rarely met with in flowering plants. The constitution of the stele of a flowering plant entirely from bundles as above described, which are either themselves leaf-traces or will form leaf-traces after junction with similar bundles, is the great characteristic of the stem-stele of flowering plants. These collateral bundles are obviously highly individualized. The external conjunctive tissue is often arranged in relation to each bundle separately, so that, for example, there may be pericyclic fibres immediately outside the phloem-masses alone. In some cases the individualization is carried further, the cortex and pith becoming continuous between the bundles, which appear as isolated strands embedded in a general ground tissue. Each bundle has its own investment of tissue corresponding with external conjunctive. The bundles sometimes keep their arrangement in a ring corresponding with the stele, though there may be no continuous cylinder. This condition is known as *astely*.



The Monocotyledons, one of the primary divisions of Angiosperms, typically possess large leaves with broad sheathing bases, containing numerous bundles. This results in the number of bundles present at any given level of the stem being high. These bundles are scattered in a definite though not superficially obvious order through the conjunctive tissue of the stele, which occupies nearly the whole diameter of the stem, the cortex being restricted to a very narrow layer, or scarcely recognizable as a definite zone. The mass of conjunctive tissue is developed as a large-celled ground-tissue, and around each bundle there is a fibrous investment. In the stems of many water plants various stages of reduction of the vascular system, especially of the xylem, are met with, and very often this reduction leads to the formation of a compact stele in which the individuality of the separate bundles may be suppressed, so that a closed cylinder of xylem surrounds the pith. The phloem is seldom so reduced, and there is normally a well-marked endodermis. In other cases the reduction goes much further till the endodermis comes to surround nothing but an intercellular channel, formed in place of the stellar tissue.

To the vascular tissue of the typical leaf and root of the Phanerogams reference is made below. But there are peculiarities of organization of the hydroids and leptoids of the bundles of flowering plants which here call for special mention. Generally the end walls of superimposed developing hydroids break down, so that the final product of differentiation is a continuous tube with lignified pitted walls. Such tubes are called *vessels*, and are characteristic of the vast majority of Phanerogams, though tracheids still dominate the Gymnosperms. There is every degree of transition between spirally thickened and reticulately thickened vessels. The sieve-tubes of Phanerogams in their most advanced forms which dominate the Angiosperms have the end walls or portions of the end walls specially perforated. Such walls are accordingly called *sieve-plates*. It is assumed that by such end sieve-plates the longitudinal movement of slimy foods is accelerated. Associated with the sieve-tubes are, in addition, cells of the same length as the sieve-tubes, generally narrow, thin walled and enucleate, and which are thought to co-operate in some intimate way with the sieve-tubes. They are known as *companion cells*, and a sieve-tube and its companion cell arise during tissue-differentiation from the same mother-cell. On the whole the leptoids and hydroids of the Phanerogams are considerably more specialized than those of the Pteridophytes.

**Stelar Tissue of Leaf and Root.**—In the leaf of the average Phanerogam the vascular tissue takes the form of a number of branching or approximately parallel, and usually anastomosing, strands, above and below which the mesophyll is raised so as to produce the so-called *veins*. The vein-system is typically very elaborate, and the bundle-system is concentrated in the leaf-stalk (*petiole*) as the tributaries of a river are massed in the main stream. The leaf-bundles are always collateral (the phloem being turned downwards and the xylem upwards), and the whole bundle may be protected above and below by fibrous cells. As the bundles are followed towards their blind endings in the mesophyll the fibres first disappear, the sieve-tubes are replaced by narrow elongated parenchyma which soon dies out, and the bundles usually end in short or long spiral or reticulate tracheids covered by the phloeothermic sheath.

The stele of the primary root of a Gymnosperm or Angiosperm is of radial structure. There are usually two or four xylem strands radially alternating with phloem strands (the stele being thus *diarch* or *tetrarch*), and the first formed xylem groups (*protoxylem*) are peripheral. A *polyarch* state is, however, common in *adventitious* roots (which arise on other stems or roots in "chance" positions), and the protoxylem groups are then numerous. The centre of the stele is seldom solid xylem, but is generally pithed, and sclerotic cells are by no means uncommon in the conjunctive tissue. The roots of some palms and orchids show a peculiar "polystelic" structure. Thus it will be seen that while the vascular systems of the stems of Phanerogams are highly individualized, those of the leaves and primary roots are of simpler organization, but are of varied structure.

**Laticiferous Tissue.**—There are, however, in certain families

of Angiosperms peculiar tissues which are not met with in the Pteridophytes. Such, for example, is the *laticiferous tissue* found in Compositae and Euphorbiaceae, which takes the form of long, usually branched tubes which penetrate the other tissues of the plant in a general longitudinal direction. The tubes possess a delicate layer of protoplasm with numerous nuclei lining the walls, while the interior of the tube (corresponding with the cell-vacuole or cavity) contains a fluid called *latex*, consisting of an emulsion of fine granules and drops of very various substances, suspended in a watery medium, in which other substances (salts, sugars, rubber-producers, tannins, alkaloids and various enzymes) are dissolved. Of the suspended substances, grains of caoutchouc, drops of resin and oil, proteid crystals and starch grains may be mentioned. Of this varied mixture of substances some are undoubtedly *plastic* (i.e., of use in constructing new plant tissue), while others are apparently end-products of metabolism, secreted within the plant-body. The relation of the laticiferous tissue to the assimilating cells, under which they often run, and the fact that where this tissue is richly developed the conducting parenchyma of the bundles, and sometimes also the sieve-tubes, are poorly developed, as well as various other facts, point to the conclusion that the laticiferous tissue has an important function in conducting plastic materials, in addition to acting as a reservoir for *excreta*. As a secondary function we may recognize, in certain cases, the power of closing wounds, which results from the rapid coagulation of latex in contact with the air. The use of certain plants as rubber-producers (notably *Hevea brasiliensis*, the Para rubber tree), depends on this property of coagulation. The trees are regularly tapped and the coagulated latex which exudes is collected and worked up into rubber. Opium is obtained from the latex of the opium poppy (*Papaver somniferum*) which contains the alkaloid morphine.

Laticiferous tissue is of two kinds: (1) *laticiferous cells*, which branch but do not anastomose, and the apices of which keep pace in their growth with the other tissues of the plant (Apocynaceae and most Euphorbiaceae), (2) *laticiferous vessels*, which are formed from rows of actively dividing (meristematic) cells. The end walls of these cells break down so that a network of laticiferous tubes arises (Papaveraceae, *Hevea*). In some cases, as in *Allium* and in the Convolvulaceae, rows of cells with latex-like contents occur, but the walls separating the individual cells do not break down.

Such facts serve to illustrate the advanced specialization of the higher plants compared with the land bryophytes, but by no means exhaust the anatomical peculiarities of the former. In particular, mention may be made of tissues which arise by modification of primary living tissues, and are accordingly known as *secondary tissues*.

#### CAMBIUM

**Secondary Tissues.**—In most of the modern Pteridophytes, Monocotyledons, and in annual plants among the Dicotyledons, there is no further growth of much structural importance after the tissues above considered have been differentiated. But in nearly all perennial Dicotyledons, and in all dicotyledonous and gymnospermous trees and shrubs, certain layers of cells retain the power of division, although they may be for long mature, and are apparently fixed elements of a tissue. By this power of growth and division they become the originators of new or *secondary tissues*, which bring in their train many modifications in the plant-body. Primary tissues which are thus awakened to new divisional activity become, like the growing points of stems and roots, *meristems* or the initials of tissues, but while the *apical meristems* of stems and roots give rise to the primary tissues above considered, these new meristems are *secondary meristems* since they give rise to secondary tissues. There are two chief secondary meristems, the *cambium* and the *phellogen*.

The cambium typically continues the formation of xylem and phloem, thus adding to the conductive tissue already produced. It is merely the cycle or band of parenchymatous tissue lying between the primary xylem and primary phloem. Its cell walls are generally thin, and as its cells enlarge by special nourishment, they are divided principally by tangential walls, thus producing



radial rows of cells. The primary xylem remains stationary, but as the cell rows thus formed increase in number and the individual cells enlarge, the primary phloem and all the external tissues move outwards. The tracts of cambium between the strands of xylem and phloem are called *fascicular cambium*, while those which cross the primary medullary rays from bundle to bundle are called *interfascicular cambium*. The cells of the interfascicular cambium likewise divide mainly by tangential walls, and with the same frequency as the fascicular cambium. Thus radially within the interfascicular cambium the primary medullary rays are left stationary, while the surrounding tissue is pushed outwards. There is usually one cylindrical layer of actively dividing cells in the cambial cylinder, and it may be imagined that at any moment it has given rise by tangential division to two such layers. The products of the interfascicular cambium may first be considered. The inner products differentiate as parenchymatous cells which are added to the medullary rays; the outer products retain the power of division. Thus the cambium is moved slightly outwards and its cells divide as before by tangential walls into outer and inner layers. The inner layer thus formed differentiates as a parenchymatous addition to the medullary ray, and the outer layer retains the power of division. Thus a general outward movement of the cambium proceeds, leaving behind or within layers of cells which radially augment the medullary rays.

From time to time it is the outer layer of cells produced by cambial activity which becomes differentiated as parenchymatous cells, while the inner layer remains cambial. In this way the outward progress of the cambium is temporarily delayed but is not arrested. After a long period of cambial activity the interfascicular cambium has moved outwards to a considerable distance, having greatly augmented the medullary ray within and radially, and to a lesser extent, but also radially, without. It will be apparent that the interfascicular cambium is not a fixed or permanent layer of cells, but that the power of division is steadily transferred outwards, and the locus of the cambium is changed with time. It will be further evident that with each step in the outward movement of the cambium the circumference of the cambium must increase. The division of the cambial cells is accordingly not accomplished solely by tangential walls, but from time to time radial divisions also occur. Thus the cambial cylinder is widened and its integrity is maintained as it moves outwards. But while in the vast majority of higher plants the additions to the medullary rays thus produced are uniformly parenchymatous, and these *primary medullary rays* increase outwards as wedges, there is some complication in the products of cambial division between the primary xylem and phloem. The fascicular cambium is generally moved outwards with the same rapidity as the interfascicular cambium, so that the cylindrical form of the cambium is maintained.

Moreover, of the inner products of division in the fascicular cambium many differentiate as *segments of a vessel*, *tracheids*, *fibres* or *parenchyma*, which may be variously grouped, but which collectively constitute the *secondary xylem*. In many instances sooner or later one or more cambial cells, within which radially such elements have differentiated, produce exclusively radial rows of parenchyma. These rows have in general the characters of medullary rays, but are obviously purely of secondary origin, and continue neither inwards to the pith nor outwards to the cortex like the primary rays. They are indeed *secondary rays* of purely cambial origin. Of the outer products of division in the fascicular cambium many differentiate as *sieve-tubes* and *companion cells*, or as *fibres* or *parenchyma* arranged in various patterns and collectively constituting *secondary phloem*. With this tissue may also be associated minor *secondary rays*, reaching inwards to the cambium, often the direct radial continuations of similar rays in the xylem, but not reaching the cortex without. It will be apparent that the tangential dimension of each tract of fascicular cambium is steadily increased as the cambium moves outwards, so that the secondary wood increases as an outward widening wedge, while the secondary phloem appears as an inward widening wedge, the two wedges meeting at the cambium. It is not to be supposed that at any moment uniform behaviour is maintained by all the

cambial cells in a longitudinal row, so that while at one level, and at various points in the fascicular cambium, secondary medullary rays are being formed in both xylem and phloem, immediately above and below this level, fibres, vessel-segments, sieve-tubes, wood-parenchyma and phloem-parenchyma are being produced. The secondary medullary rays are accordingly of no great depth, and may well be described as narrow bands of parenchyma placed radially in the xylem and phloem. Similarly the behaviour of the interfascicular cambium is not uniform at all levels or at all stages in its outward progress, for while for a time it may produce parenchyma exclusively, locally its products may be secondary phloem and secondary xylem. Thus after a time an island of secondary wood and phloem is seen in a cross section of the stem, dividing the primary ray into two branches, which, when followed outwards, reach the cortex. Nor are the primary rays of great depth, though on an average they are much deeper than the secondary rays, for the downward course of both xylem and phloem is tortuous, and fusion of strands occurs above and below the rays, which are accordingly of lenticular outline when seen in a tangential section of the stem.

**Annual Rings.**—In those plants whose annual activity is interrupted by a regular winter or dry season the limit of each year's increment of secondary wood, and to a less obvious degree of secondary bast, is marked by a more or less distinct line which is produced by the sharp contrast between the elements formed in the late summer of one year and those produced in the spring of the next. It is believed that in relation to the large and rapid supply of water and other substances to the unfolding leaves in spring and early summer, large vessels are produced by the cambium in the spring, while as summer advances and the need for water diminishes, the vessels formed are narrower, and as the supply diminishes still further, more abundant fibres, with greatly reduced cavities, arise. Thus in a single season of cambial activity a rough outward progression may be traced in the secondary wood of that season from wide vessels to narrow fibres, beyond which the transition to the wide vessels of the succeeding spring is sudden. Each zone thus recognized in a cross section of the stem is called an *annual ring*, and the lines of separation of successive rings mark the temporary halting places of the cambium at the end of successive seasons.

**Sap-wood and Heart-wood.**—The older wood of large trees, forming a cylinder in the centre of the trunk, frequently undergoes marked changes in character. The wood-parenchyma and medullary rays die, and the walls of all the cells often become greatly hardened, owing to the deposit in them of special substances. Wood thus altered is called *heart-wood* or *duramen*, as distinguished from the younger *sap-wood* or *alburnum*, which is nearer the cambium, carries on the active function of conduction, and retains its parenchymatous cells in life. The heart-wood ceases to be of any use to the tree except as a support, and owing to its dryness and hardness is much used for industrial purposes.

**Phellogen and Periderm.**—It will be obvious that secondary increase of xylem and phloem involves an outward movement of the primary phloem and of all the elements which surround the latter, and that the cortex, and particularly the epidermis, must accommodate for this movement, either yielding passively to a limit and being injured or destroyed by the outward pressure, or being to some extent modified so as to persist. In most cases the epidermis is unable to maintain the active radial division of its cells necessary for such expansion as occurs, is soon stretched to its limit, dies and is destroyed. Extensive radial division in the cortical cells is progressively less essential as the inner cortex is followed inwards, and as a rule, by a combination of radial and tangential divisions, the integrity of the cortex is maintained. Towards the periphery of the cortex, and commonly by modification of its outer layer, a secondary meristem, similar to the cambium, arises and produces external and internal secondary tissues. This meristem is the *phellogen*, and the whole of the tissue it gives rise to is known as *periderm*. The phellogen derives its name from the fact that its external product is the characteristic tissue known as *cork*. This consists typically of closely fitting layers of cells which quickly die, and when mature, have



completely suberised walls which collectively serve to replace the epidermis as an external protective layer, when the former is ruptured. The outer layers of the cork are constantly being destroyed, but new layers are in progress of formation within. The internal tissue formed by the phellogen is known as *phellogen*; it augments the cortex, and typically consists of living parenchymatous cells to some extent capable of further division. Indeed, an inward succession of phellogens may arise in the phellogen and in even more deeply seated living layers. In certain cases the epidermis becomes the phellogen. To the great activity of the phellogen, and to the power of formation of a series of phellogens in deep layers, the value of the cork oak as a source of cork is due.

**Cambium in Roots.**—The cambium in the root, which is generally found in those plants which have a cambium in the stem, always arises in the conjunctive tissue internal to the primary phloem, and forms new (secondary) phloem in contact with the primary and secondary xylem internally. In roots which thicken but slightly, and whose cambium usually appears late, it is confined to these regions. If the development of secondary tissues is to proceed further, arcs of cambium are formed in the pericycle external to the primary xylem, and the two sets of cambial arcs join, forming a continuous, wavy line in transverse section, with bays opposite the primary phloems and promontories opposite the primary xylems. Owing to the resistance offered by the first formed secondary xylem, the bays are pushed outwards as growth proceeds, and the wavy line becomes a circle. Opposite the primary xylems the cambium either (a) forms parenchyma on both sides, making a broad, secondary (principal) ray, which interrupts the vascular ring and is divided at its inner extremity by the islets of primary xylem, or (b) forms secondary xylem and phloem, completing the vascular ring. In either case narrow secondary rays are formed at intervals, just as in the stem. Thus the structure of an old thickened root approximates to that of an old thickened stem, and so far as the vascular tissues are concerned, can often be distinguished from the latter only by the position and orientation of the primary xylem.

**Growing Points.**—The tissues above considered all owe their origin ultimately to the growing points or *apical meristems* defined in the embryonic plant-body. To the great variety of apical meristems found in vascular plants reference alone can here be made. It must suffice to note that in most Pteridophytes there is a single large apical cell at the end of each stem- and root-axis, that it usually has the form of a tetrahedron, that its base occupies the surface of the growing point, and that its apex points inwards. By definite and regular divisions of such a cell a mass of still undifferentiated cells is produced immediately behind the growing point, which is continuously occupied by a residual apical cell. From these undifferentiated cells the tissues above considered sooner or later arise by further growth, divisions and differentiation. In most Phanerogams the *apical (or primary) meristems*, instead of consisting of single apical cells or of a definite group of initials, are stratified, *i.e.*, there is more than one layer of initials. Throughout the Angiosperms the epidermis of the shoot originates from separate initials which never divide tangentially, so that the young shoot is covered by a single layer of dividing cells, the *dermatogen*. Below this are the initials of the cortex and the central cylinder. Whether these are always in layers which remain separate is not known, but it is certain that in many cases such layers cannot be distinguished. This, however, may be due to irregularities of division and displacement of the cells by irregular tensions, destroying the obviously layered arrangement. In some cases there is a perfectly definite line of separation between the young cylinder (*plerome*) and young cortex (*periblem*), the latter having one or more layers of initials at the actual apex. The separation of layers in the apical meristem of the root is usually much more obvious than in the stem. The outermost layer is the *calyptrogen*, which gives rise to the root-cap, and in Dicotyledons to the piliferous layer as well. The periblem, one cell thick at the apex, produces the cortex, to which the piliferous layer belongs in the Monocotyledons; and the plerome, which is nearly always sharply separated from the

periblem, gives rise to the vascular system.

There is generally some definite progression in the actual differentiation of the individual tissues, so that, for example, comparatively simple xylem and phloem elements may be recognized in certain portions of a stem or root before the differentiation of xylem and phloem is accomplished in the stele as a whole. Such first formed xylem and phloem elements are known respectively as *protoxylem* and *protophloem*, and serve for the initial conduction of food-materials, while the later formed elements of the primary xylem and phloem are called respectively *metaxylem* and *metaphloem*.

The branches of the stem arise by multiplication of the cells of the epidermis and cortex at a given point, thus forming a protuberance at the end of which an apical meristem is organized. The vascular system is connected in various ways with that of the parent axis by the differentiation of bundles across the cortex of the latter. This is known as *exogenous* branch formation. In the root, on the other hand, the origin of branches is *endogenous*. The cells of the pericycle, usually opposite a protoxylem strand, divide tangentially and give rise to a new growing point, the outward path for which is prepared by digestion of the surrounding tissues. The connections of the stele of such a root with that of the parent axis are made across the pericycle of the latter. The cortex of the new root is never connected with that of the parent, but with its pericycle. *Adventitious roots*, arising from the stem, usually take origin in the pericycle, but sometimes from other parts of the conjunctive tissue.

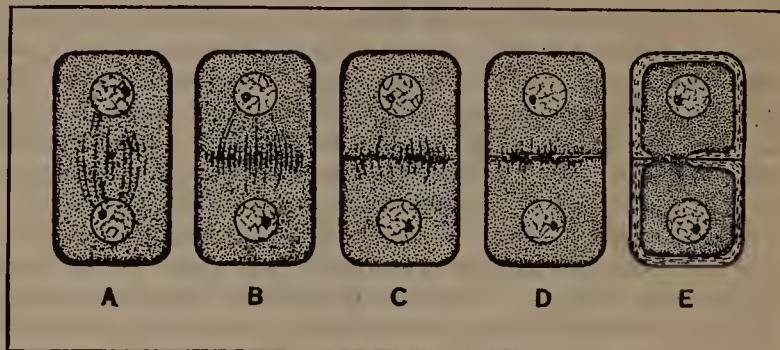
Thus it will be seen that throughout the vascular plants there are definite and orderly methods of production and distribution of the tissues destined to play their parts in the major or minor processes of life, and that such organisms are well fitted for life on land.

(J. McL. T.)

## CYTOLOGY

The structure and development of the vegetable cell so far as the protoplasm and the nucleus are concerned are considered in their broader aspects in the article CYTOLOGY.

The recognition of the fundamental similarity of the cells of plants and animals and the identity in structure and functions of animal and vegetable protoplasm which formed the starting point in the study of cytology are conceptions which subsequent investigations have only broadened and confirmed. Nevertheless this agreement, whether it be in the minute structure of the protoplasm or in the details of nuclear mitosis, is accompanied by peculiarities in the cell structure of plants which have had a profound influence in the evolution of the vegetable body. Of these the most important, because far-reaching in their effects, are the presence of



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### FIG. 1.—DEVELOPMENT OF THE CELL WALL IN A VASCULAR PLANT

A. Telophase of mitosis in meristematic cell, B. Appearance of swellings on the achromatic fibrils, C. Fusion of swellings to form an equatorial cell plate; fibrils disappearing, D. deposition of new primary wall (middle lamella) between the halves of the split cell plate, E. deposition of a secondary wall layer between the plasma membrane and middle lamella, except in region of a large pit. Primary wall, solid black; cytoplasm stippled, plasma membrane densely stippled; secondary wall shaded

plastids in the protoplasm and the existence of the cell wall. In the higher plants the egg is necessarily a naked cell, but when fertilization is accomplished the new cell secretes around itself a membrane—a cell wall—before it begins to grow and divide, and the myriad cells to which it gives rise in the course of its further development are from the first enclosed in a similar membrane.



The continuous development which is such a characteristic feature of the structure of the higher plants depends on the presence of persistent embryonic regions or growing points at such places *e.g.*, as the tips of stems and roots. This enables us to study in these regions the formation of new cells, and to trace their development and modification to form the adult tissues of the member to which they belong.

The individual cells appear rectangular in form and consist of a mass of protoplasm containing a large nucleus and separated from the neighbouring cells by a delicate membrane. It is unnecessary to refer to the detailed structure of the protoplasm and the nucleus, since these have already been fully described (*see* CYTOLOGY), but with suitable treatment it is possible to distinguish in the protoplasm of these meristem cells the rudiments of definite protoplasmic organs, the plastids. The nature, purpose and function of these important bodies will be considered below: for the present it is sufficient to say that they are differentiated portions of the protoplasm which perform definite functions.

From such embryonic cells all the tissues of the plant body are formed by processes of growth and differentiation. Growth involves an increase in size of the individual cells which may in some cases result in an enlargement to many thousand times their original volume. This enlargement does not however necessitate a proportional increase in all the parts of the cell. Increase in size is mainly the result of active extension of the cell wall. The protoplasm does not increase in volume in the same proportion and hence cavities appear in it which are filled with a watery fluid—the cell sap. As the wall enlarges these spaces or vacuoles increase in size and number and eventually coalesce to form one large central vacuole in the protoplasm which thus becomes restricted to a comparatively thin layer closely applied to the cell wall (fig. 1, E). The nucleus, which undergoes little change during this process or may even be reduced in size, is at all times embedded in the protoplasm and thus comes to lie close to the cell wall or in some cases it may be slung by delicate protoplasmic strands in a more or less central position in the cell. It is often possible to observe a circulation of the material in these strands, definite streams moving from the cell wall towards the nucleus and vice versa. It is, however, uncertain as to whether this is a general phenomenon.

**The Cell Sap.**—The cell sap which fills the vacuoles is water in which are dissolved substances of various kinds, some of which are food materials others products of the metabolism of the protoplasm. Its composition is constantly changing but among the substances of constant occurrence are inorganic salts, carbohydrates such as the sugars and soluble nitrogenous compounds; in addition the sap of fully developed cells may contain colouring matters such as the anthocyanins, which are red, violet, or blue and give their characteristic colour to the petals of many flowers, the leaves of such trees as the copper beech and the tissue of the beetroot. The large proportion of the total volume of the cell occupied by the cell sap explains the large percentage of water present in soft vegetable tissues; *e.g.*, cabbage and spinach leaves, roots of turnip and beet and shoots of asparagus contain over 90% of water.

The cell wall and the protoplasm are both freely permeable to water and indeed the former is also permeable to the molecules of crystalloid substances. The living protoplasm, however, may be described as semi-permeable since it may restrict the passage of dissolved substances either into or out of the vacuole. One result of this property of the protoplasm is that, whereas at a given moment the pressure of molecules of water inside and outside the cell may be equal, there may exist in the vacuole in addition a pressure due to the molecules of the salts; the cell is in consequence distended, the wall is stretched and owing to its elasticity exerts a counter-vailing pressure. Such a cell is described as turgid and in this condition it acquires a certain rigidity analogous to that of a distended air bladder.

This characteristic of the vegetable cell has played an important part in the evolution of the plant body since it has rendered possible the development of plant organs of relatively large size with a minimum organization of skeletal tissue. Such structures as the leaves of herbaceous plants—though provided with a network of

veins—maintain their form and position only by the turgidity of the living cells of which they are largely built up. Loss of water from the individual cells results in a shrinkage of the tissues as a whole, and the familiar appearance of wilting or flagging of plants deprived of water is brought about in this way.

**Plastids.**—The plastids or chromatophores are portions of the protoplasm which have become specialized for the performance of certain functions. They are readily distinguished in the adult cell by their size and definite form and they are often conspicuously coloured. Leucoplasts are colourless and occur in the cells of the deeper lying tissues where light cannot penetrate—if exposed to light they often become green. They are frequently concerned with the formation of starch grains. Chromoplasts are colour-carrying bodies giving red and yellow colours to the petals of flowers, ripe fruits, etc.; they contain yellow and red pigments such as xanthophyll and carotin. The most important of all the plastids, however, are the green chloroplasts, chlorophyll bodies or chlorophyll corpuscles as they are variously termed. They contain chlorophyll and are of universal occurrence throughout the vegetable kingdom with the sole exception of the important group of the Fungi. It is by means of this pigment that the plastids are enabled in the presence of light to form carbohydrates from water and carbon dioxide.

The importance of this process cannot be overestimated, since it is the starting point in the manufacture of the food of all living organisms and its activity has made possible the existence of plants and animals upon the earth. (*See* PHYSIOLOGY.) Chlorophyll when extracted from plants by suitable solvents can be shown to contain a number of pigments. The green, blue-green, yellow and red have been already mentioned. In form the chloroplasts are extremely variable and the Algae (*q.v.*) show a rich variety of shape; in the higher plants however they are discoid in form. Like the leucoplasts they frequently show inclusions of starch grains. They may increase in number by dividing into two halves by simple constriction. They have been shown to be present in the egg cell of some plants and are, in these cases, thus passed on from one generation to another, but they have not been demonstrated in the sexual cells of all plants.

**The Cell Wall.**—The cell wall in meristematic cells is an extremely delicate membrane but, with the completion of the growth in size of the cell, it is increased in thickness and may in certain cases undergo considerable modification. It is commonly regarded as a secretion of the protoplasm and it is in living cells in intimate relation with the protoplasm which may interpenetrate the particles of its substance. This close relation can be readily appreciated when the process by which the wall is first laid down is considered. From the beginning of the plant's existence as a single cell, all new cell formation consists in the division of a pre-existing cell into two halves by the formation of a dividing wall. In this process the cytoplasmic spindle which functioned in the preceding nuclear division (*see* CYTOLOGY) plays an important part. The spindle fibres—increased in number—show swellings or thickenings in the middle of their length (fig. 1, B), which coalesce and form a continuous "cell plate" which is extended until it reaches the side walls of the mother cell. This cell plate is not however the cell wall; it is of protoplasmic nature and splits into two layers between which the true wall substance is laid down (fig. 1, D). The subsequent growth of the cell wall is facilitated by its intimate penetration by the protoplasm, which lays down fresh materials between the existing particles (intussusception), and later adds to its thickness by the deposit of fresh layers of material on the inner surface of the primary wall (apposition).

The primary wall, laid down in the manner above described, might be regarded as common to the two cells concerned in its formation, but many facts go to show that it is either a double membrane from its inception or that it readily splits into two. The result is that every cell is surrounded by its own individual wall. This is seen very clearly in the development of elongated cells such as fibres, which may grow to many hundred times their original length. In this process they may change their position, sliding over the surface of neighbouring cells and making contact with cells of different, and of more remote, origin. Such elongated



cells as the fibres undergo considerable thickening of their walls when their growth is completed. This thickening is originally of cellulose, but it may undergo secondary changes becoming wholly or in part lignified, thus rendering the wall firm and hard and better adapted to serve the purpose of mechanical support. Thickening and lignification of the wall is also characteristic of the cells concerned in the formation of the water-conducting elements. With the completion of these changes in the cells of the strengthening and water conducting tissues the protoplasm disappears and the walls alone remain.

**Plasmodesma.**—The living cell in a complex multicellular plant body is a unit, but not an independent one, and its functions must be conditioned by, and related to, the activities of the organism as a whole. This must involve a close connection between the living protoplasm of neighbouring cells and this is effected by delicate connecting strands, the plasmodesma, which traverse the walls. These represent in some cases the persistence of the original continuity of the protoplasm of two sister cells, but for the most part they are probably new contacts established when growth is completed. The presence of these delicate connections has been established in a large number of cases, and it is probable that they are of universal occurrence in the higher plants. They play a part in the correlation of the functions of the cells, and they may also provide the means by which stimuli can be conveyed through long tracts of tissue in those cases, where the region stimulated is distant from that in which the response is shown.

(R. J. T.)

### DISTRIBUTION AND ECOLOGY

The distribution of plants can be considered from two main aspects. The present or past distribution of species, genera and families, termed *floristic plant geography*, can be studied both for its own sake and as a factor in determining the location of human activities or features of the earth's surface. But besides this purely geographical aspect the facts of distribution can be considered in relation to their causes; the influences of climate, of topography, of the soil conditions, of other plants, of animals, and even of the past history of the superficial crust of the earth and of the species itself. It is this relation of plants to their environment, in its widest sense, and the mutual effect of environment and organism, which is the province of *ecological plant geography*, or briefly plant ecology.

**Floristic Distribution.**—The floristic distribution of species exhibits the greatest possible variation from the species which as a wild plant is confined to a limited area (*endemic*) to wide-ranging species such as many microscopic plants (e.g., some bacteria) which are apparently universal in their occurrence. There are probably no vascular plants that are strictly cosmopolitan, but the common bracken (*Pteridium aquilinum*) and the reed (*Phragmites communis*), though far less common in the tropical regions, are feral species in the most diverse climes (the former, however, notably absent from oceanic islands). In striking contrast are such plants as the fern *Thyrsopteris elegans*,—an endemic confined to the Island of Juan Fernandez or *Pringlea antiscorbutica* restricted to the tempestuous shores of Kerguelen.

Endemics are an especial feature of oceanic islands as is shown by the flora of Madagascar, which comprises some 4,000 species of vascular plants and contains no less than 75% of endemics. In New Zealand the proportion of endemics is 74%, whilst in Hawaii the endemics constitute 80% of the entire flora. By contrast the floras of continental islands are practically destitute of endemics, as is shown by that of Britain, which amongst its flowering plants probably includes but one endemic of specific rank, namely, the wolf's-bane (*Aconitum anglicum*).

It is clear that when a new species originates it will not immediately attain its climatic limits but its spread will be a gradual process, occupying a longer or a shorter time according to the efficiency of the means whereby the dispersal of its seeds or other reproductive bodies is attained. It is the belief that this process is in general secular rather than rapid, which has led to the view that the area occupied by a species, genus, or family is roughly dependent upon its age. Willis has adduced evidence to show that the

majority of endemics are species of recent origin which have either not had sufficient time to spread over a larger area (e.g., local endemics in continental areas) or have been prevented, by the presence of natural barriers, extending beyond their place of origin. The latter explains the high proportion of endemics on oceanic islands. On the other hand, it is certain that some endemic species are relics of a former more extensive area of occupation, the remnants of a bygone vegetation. The fern genus *Matonia* is at the present day represented by three species, of which two are confined to Borneo and the third also occurs in the Malay Peninsula; yet fossil evidence indicates that ferns of this affinity had an almost cosmopolitan distribution in Mesozoic times. The *Gleicheniaceae*, the *Schizeaceae*, and *Marattiaceae*, families of ferns now practically absent from the northern hemisphere, furnish further examples of area diminishing with the lapse of time. Amongst the flowering plants the present restricted distribution of *Ginkgo biloba*, the tulip tree (*Liriodendron tulipifera*) and the sequoias, affords a marked contrast to the widespread occurrence of species of these genera in Tertiary times and shows the importance of the past history of a group in appreciating the significance of the existing representatives.

Frequently the members of a genus comprise one or more species which extend over a large area, whilst the remainder are of much more restricted distribution and occupy areas either included in or overlapping the range of their more widespread congeners. Illustrations are furnished by the she-oaks of Australia (*Casuarina*), with the littoral *C. equisetifolia* extending from east Africa and Madagascar to the Society islands and Burma and the Philippines to Tasmania, within which area occur a number of other species. Again the genus *Mercurialis* includes the dog's mercury (*M. perennis*) and *M. annua*, which are of wide range, whilst the five or six other species extend over comparatively small areas in the Mediterranean region and eastern Asia. It is probable that in such genera the species of more local occurrence are derivatives of the wide-ranging types, but it is also evident that were the widely dispersed parent types to die out the other species of restricted distribution would come to present the condition of discontinuous distribution which is a feature of many genera and families at the present day. The pipeworts (*Eriocaulon*) are chiefly found in tropical and sub-tropical regions, but *E. septangulare* is found in the eastern United States, the west of Scotland, and the west of Ireland. Of over 400 species of heath belonging to the genus *Erica*, the majority are concentrated in Cape Colony and the Mediterranean area. The *Proteaceae* and *Cycadaceae*, containing many very localized genera, now exhibit a discontinuous distribution in tropical and sub-tropical regions, but there is little doubt that the *Cycadaceae* extended over a large part of the world in Jurassic times and the *Proteaceae* were probably much more widely distributed in the Tertiary epoch than at the present day. Discontinuous distribution in the species may be the outcome of irregularities of dispersal, the result of extinction from parts of its former range, or even due to origin of the species in more than one locality.

**Effects of Glaciation.**—It is quite impossible to appreciate the present distribution of species in either North America or northern Europe without recognition of the profound changes consequent upon the last glacial epoch. During Cretaceous times there would appear to have been a remarkable uniformity in the character of the vegetation of the world, with warm temperate types as far north as Greenland. This uniformity was succeeded by a differentiation in the Tertiary period. On either side of the tropical belt there probably existed a zone of forest presenting a mixture of temperate and subtropical types, southern types being present in the northern hemisphere and northern types, such as the true beeches and the common oak (*Quercus Robur*), being present in the southern hemisphere. Mrs. Clement Reid has admirably demonstrated, by a comparison of successive floras of the Pliocene period of Europe, the gradual disappearance of exotic types as the Pleistocene approached, probably accompanying a diminution of temperature. It is due to the work of Heer on the arctic fossil flora, the writings of Asa Gray, Saporta and Hooker that the fossil floras of the past have been so ably util-



ized in the elucidation of the peculiarities of the distribution of the present. The holarctic distribution of a large assemblage of species prior to the glacial refrigeration is the clue to the resemblances between the American and east Asiatic floras. Of these migrants, driven southwards by the increasing cold, relics remain in the genus *Sequoia*, now only represented by two north-west-American species, in *Ginkgo biloba*, confined to western China, in the American genus *Liriodendron* and the Chinese *Glyptostrobus*. The magnolias no longer occur wild in Europe as they did in the past, but still survive both in Asia and America. Of the genera cited Depape has recorded Pliocene remains from the valley of the Rhone of *Sequoia sempervirens*, *Liriodendron tulipifera*, *Ginkgo biloba*, and *Glyptostrobus heterophyllus*. The elimination of these and many others from the European flora is probably to be attributed mainly to the presence of natural barriers against the southward retreat, such as the Mediterranean, whereas in Asia and America there was a continuous land bridge to a climatic sanctuary, the temporary home of some, the permanent retreat of others.

During the Ice age itself the flora consisted of definitely arctic types and a considerable number of other hardy species which survived the cold in the areas, probably of considerable extent, which were not actually covered by ice. Judged by the frequency of the remains in sub-fossil deposits of the glacial period in Europe the commonest species were the mountain dryas (*Dryas octopetala*), the dwarf birch (*Betula nana*) and various willows of mat-like habit, such as *Salix reticulata*, *S. polaris*, etc. It is noteworthy that the species cited and a number of others prevalent at that period are now most characteristic of arctic regions but also occur in warmer climates on what may be termed arctic islands, namely, the summits of the higher mountains, a discontinuous distribution that can be attributed to survival from glacial times. With the final retreat of the ice, which in northern Europe probably took place somewhere about 14,000 years ago, the recolonization of the glaciated areas by the less hardy species began.

The colonization thus begun has continued ever since. The fact that Ireland possesses but two-thirds of the vascular plants of Britain whilst the flora of England, though richer than that of Scotland, is less varied than that of the neighbouring areas of France emphasizes the importance of the facilities for dispersal of fruits and seeds in determining the distribution of species. The rapid spread of the Canadian pondweed (*Elodea canadensis*) from Market Harborough, where it first appeared in England in 1847, of *Veronica persica*, or more recently of the rayless mayweed (*Matricaria suaveolens*), a native of Oregon, all of which have become abundant over a great part of Britain; or, again, the spread of the prickly pear (*Opuntia inermis*) at the rate of a million acres a year in Australia and the choking of the waterways of Florida by the water hyacinth (*Eichornia crassipes*) all bear witness that area is not necessarily a criterion of age and that the process of colonization is still going on, a process in which the disturbing influence of the hand of man plays no small part.

**Ecological Factors.**—The most superficial observation shows that species are not uniformly distributed throughout their range and that certain conditions favour one kind of plant rather than another. In the ecological concept the idea of competition is never absent and the effect of the external conditions upon the constituents of the vegetation of any region is largely dependent upon their selective action. The sum total of the external circumstances surrounding the plant is termed the *habitat* and the various conditions that together determine distribution are termed the *habitat factors*, of which some are physical and others biological.

**Climatic Factors.**—Of the physical factors the most important are climatic and of these temperature would appear to play the major rôle. Hence we find that the main vegetation zones on the earth's surface have a latitudinal distribution and that the species which has an extensive north and south range has commonly a wide range in the east and west direction also. Whilst some species, as already noted, are almost cosmopolitan, it is true of the majority that they do not occur both in tropical and arctic regions. In some cases it has been shown that the species com-

prises several geographical races with different capacities for endurance of climatic extremes, but there is little evidence to show that species can become adapted to climatic extremes that they could not initially endure. Many garden plants are cultivated in the open beyond the limits of their natural range, showing that the climatic conditions need not be lethal in order to delimit the area of a species.

By diminishing the rate of growth or inhibiting reproduction temperature may effectually prevent the maintenance of a species in competition with other plants although there is a considerable margin before the lethal limit is reached. Extremes of temperature, however, cause death in many plants by coagulation of the living cell contents, and in general the susceptibility to such extremes is directly proportional to the amount of water which the plant or part of the plant contains. Hence seeds which have a very low content of water are exceptionally resistant whilst succulent shoots are especially susceptible. Rapid changes of temperature are far more liable to prove fatal than changes of the same amplitude which occur slowly.

In tropical and sub-tropical regions where there is no dry season the vegetation consists of broad-leaved evergreen forests, but where, as in temperate latitudes, a warm and cold season alternate, the characteristic type is deciduous woodland; whilst in still higher latitudes, where the growing season, or frostless period, is of short duration, the prevailing types of forest consist of narrow-leaved evergreen conifers. A similar zonation to that presented from the Equator to the Poles is seen in the altitudinal zonation on the higher mountain masses. Such is well illustrated in Corsica where the olive characterizes the belt from sea-level to 400 metres, the chestnut from 400m. to 1,000m., pines (*P. Pinaster* and *P. Laricio*) and beech from 1,000m. to 1,600m.; the alder (*Alnus suaveolens*) the sub-alpine zone from 1,600m. to 1,900m. and scrub of the dwarf juniper (*Juniperus nanus*) with *Berberis aetnensis* up to 2,000 metres.

The importance of temperature and the length of the growing season is further shown by the altitudinal distribution of individual species, which varies markedly in correspondence with the latitude. For example, *Polygonum viviparum* attains to 1,230m. in Scotland at 56.48 N. Lat., on the Swiss alps it is found at over 2,850m. (9,000ft.), and on Mt. Everest (27.59 N. Lat.) reaches an elevation of 4,460m. (14,500ft.). Study of comparative altitudes in different latitudes shows that the upper limits tend to rise on the higher mountains and in areas of large mountain masses, which indicates the importance of exposure conditions.

The extreme conditions tolerated by living vegetable organisms is shown by the fact that spores of bacteria can endure immersion in liquid air whilst certain blue-green algae (*Phormidium laminosum*, *Mastigocladus laminosus*) occur in water at temperatures above 49°C. Even amongst the flowering plants the resistance of some species to cold is considerable, *Larix siberica* for instance growing where temperatures of -70°C are not unknown, whilst seeds are particularly resistant to both heat and cold. Here, too, attention may be called to the extreme altitudes attained by some flowering plants, *Arenaria muscosa* being found at 20,400ft. on Mt. Everest, the highest recorded station for a member of this class.

**Precipitation.**—Of almost equal importance to temperature is the amount and seasonal distribution of precipitation either in the form of rain or snow or as dew and fog. In regions of equivalent temperature forests will in general occupy the areas of highest precipitation, deserts the areas of lowest precipitation, and grasslands the areas of intermediate humidity. In the United States, for instance, the mean annual rainfall in the desert region ranges from 0-30in., in the prairies from 20-30in., and in the regions of forest from 30-90in. In any estimate of the influence of rainfall, however, the humidity of the air is necessarily a considerable factor and the efficacy of a given precipitation will be largely influenced by the temperature changes, upon which the rate of water-loss from the surface of the plant and from the soil in which it grows so largely depends. Further, this water-loss will be greatly augmented by wind, and so the velocity and frequency of air movements have an important influence on the



limits of species and plant-communities. The frequent incidence of high winds inhibits the growth of trees near the summits of mountains, both by their drying action and mechanical effect, whilst the strong winds and low temperature together determine the distribution of arctic Tundra.

**Illumination.**—Since all green plants manufacture their organic food by means of the radiant energy absorbed from sunlight, the intensity and duration of this illumination naturally affects the distribution of species. Many woodland plants are so constituted as to function best in this respect when growing in comparatively weak illumination, whilst others, such as many littoral species, attain their optimum rate of food production in full sunlight. Even the weak light which reaches the floor of a woodland is sufficient for the requirements of some mosses, but when the shade is too intense the vegetation is confined to parasites and saprophytes and so the rich fungus flora of a dense beechwood or pinewood becomes one of its salient characteristics. It has, moreover, been found that the length of the period of daily illumination may be an important factor in influencing reproduction. Some species appear to be indifferent to the length of the period of daylight, except in so far as the amount of organic food they manufacture is dependent on the total radiant energy they receive. Other species respond to a shorter daily illumination by earlier flowering and fruiting, whilst with still other species the effect is a retardation in the reproductive process.

Nevertheless, though the individual climatic factors play each their separate part, it is mainly upon their interaction that distribution of species depends. Thus it is that some are particularly associated with oceanic climates characterized by small amplitude of temperature and high humidity, whilst others are found in the drier and more extreme conditions of continental areas. Examples of the former are furnished by the petty whin (*Genista anglica*) and the wild hyacinth (*Scilla nutans*), features of the west of Europe, whilst the latter are represented by various species of *Eryngium* and *Artemisia* of the Russian steppes.

**The Soil.**—The character of the soil is chiefly important as to its physical structure, except where the chemical constitution exhibits extreme conditions. For upon the size of the constituent mineral particles and the proportion of organic material which the soil contains depends in large part its capacity to retain the water which reaches it in the form of precipitation or by capillarity. It is the feeble power of such retention that renders the conditions on a sand dune or a shingle beach comparable to those of a desert even in regions of high precipitation and humidity. It is in great measure differences in *water capacity*, as this power of water retention is termed, that are responsible for the different types of vegetation on clay, sand, and peat, within an area of uniform climatic conditions. Nevertheless, other soil factors, such as the chemical nature, the reaction, the nature of the soil atmosphere and the constitution of the teeming population of micro-organisms, etc., all play a part in determining the relative suitability of soils for one species or another. The soil conditions in untouched vegetation, however, present a very different distribution from the comparative uniformity of agricultural land, a definitely stratified organization, as a consequence of which species growing intermingled but with root systems of differing depths of penetration may be occupying very different types of soil both as regards chemical and physical constitution. The direct influence of the chemical nature of the soil is often difficult to separate from its indirect influence on water supply, absorption of soluble salts, etc. This is well seen in the vegetation of calcareous and non-calcareous soils. The so-called calcicole species which frequent the former may prefer calcareous soils either because of their physical qualities, because of their neutral or slightly alkaline reaction, or because of their chemical properties. Further, such association may be obligatory or merely preferential. Preference for a particular soil type is sometimes a feature of an entire genus, as that of *Clematis* for calcareous soils, whilst in other groups closely allied species may have very different requirements.

**Biological Factors.**—These comprise the effects of plant on plant and the relation between animals and plants. Of these biological factors, however, the most important is the influence of

man. It is largely due to man that the present tree limit in the alps is considerably below its former altitude, whilst even in comparatively unsophisticated regions of the tropics considerable changes have resulted from the practice of migratory cultivation and the artificial extension of grassland at the expense of forest, both for domestic animals and the encouragement of wild game. The profound effect of rabbits on natural vegetation has been well exemplified in New Zealand and Australia, whilst the attacks of field mice, mollusca and various parasitic fungi, *inter alia*, considerably affect the efficiency of reproduction in many wild species. On the other hand, the beneficial effects of earthworms, moles, ants, etc., is analogous in nature to the action of the plough in maintaining adequate aeration of the soil. Many flowers depend upon insects for their pollination, and hence the area of a species may be restricted by that of its pollinating agent.

In addition to the effects of climatic, edaphic (soil), and biotic factors, there are the historical factors to which allusion has already been made, and in this connection it must be recognized that the vegetation of yesterday has in large part been responsible for the conditions which determine the vegetation of to-day. The habitat is not static, but dynamic, and the present is but the link which joins the conditions of the past to those of the future.

**Autecology.**—The success or failure of the individuals of the species in one area will depend not merely on its ability to flourish in the environment there present but also on its capacity to modify that environment and itself to become modified. The study of this relation of the individual to its surroundings is termed *autecology*. A few examples will serve to illustrate the importance of the life history and structure of the organism in determining its fitness for a particular station or habitat. Thus annuals are an especial feature of deserts, where the short relatively wet season is occupied in rapid growth and reproduction whilst the dry hot season is passed in the seed state. The same quality has enabled many plants to become weeds of arable land and others to survive the rigours of a cold season. By contrast the vegetation of arctic regions is characteristically rich in perennials, for the growing season is so short and the temperature so low that growth is a slow process, and the annual species which occupies a considerable period in attaining the reproductive state is at a disadvantage in competition with perennial types in which the flower rudiments are often formed already in one season preparatory to their expansion in the next. Many of the herbaceous plants of woodlands exhibit exceptionally early leaf expansion, and hence their leaves are receiving light and manufacturing food material for weeks, and sometimes months, before the canopy of foliage of the shrubs and trees is formed above. This quality of precocious leaf development has enabled its possessors to occupy woodlands in which the light intensity during the summer months may be less than 1% of that in the open.

The possession of a relatively small leaf surface, a tufted habit, low growth, or hairy leaves are a few amongst many external features which tend to reduce the rate of water loss from the leaf surface (transpiration) and thus enable their possessors to occupy drier areas than would be possible for them in their absence. Such features are often accompanied by a microscopical internal structure also tending to check the rate of water loss, and plants having an aggregate of such feature are often termed *xerophytes*, from their capacity to grow in arid situations. Many plants, on the other hand, are entirely devoid of such transpiration checks and even exhibit features which tend to promote water loss, and often possess means of secreting liquid water. Such plants are quite unsuited to dry situations, but are admirably adapted for the humid situations in which they flourish.

Some species owe their success to a remarkable capacity for vegetative spread, as, for example, *Mercurialis perennis* and *Epilobium angustifolium*, others to a copious seed output, as, for instance, the foxglove (*Digitalis purpurea*), of which one plant may produce a million seeds in a single season. Contrast this with the seed output of another woodland species, *Allium ursinum*, which often does not exceed 40 seeds per annum. The rosebay willow-herb (*E. angustifolium*) will often spread at the rate of 60cm. a year by means of its rhizomes and at the same time produce



some 50,000 seeds, whereas its congener, *E. montanum*, only produces from 4,000 to 13,000 seeds in a season and spreads vegetatively about 1 cm. per annum. The equipment of species in the struggle for existence is thus very unequal.

**Seed Dispersal.**—Many seeds and fruits are dependent on wind action for their distribution, and some, such as the parachute-like fruits of the goatsbeard (*Tragopogon*), the plumed seeds of the willows and willowherbs, or the winged seeds of the tropical *Bignoniaceae*, are wonderfully fitted for this mode of dispersal. Others, such as the burr-fruits of the goose-grass (*Galium aparine*), enchanter's nightshade (*Circaea*) and herb bennett (*Geum urbanum*), become attached to the coats of animals by means of their hooked appendages, whilst the seeds of many berries are swallowed by animals and deposited in their droppings, often at great distances from their source. Here, however, it should be noted that the crops of birds on migration are usually empty and their plumage remarkably clean, so that bird carriage is not so important an agent as might be supposed. Still other seeds or fruits, like those of many waterside plants, have a buoyant structure and are carried to new habitats by means of streams and ocean currents. The efficacy of this means of dispersal is shown by the carriage of seeds of *Entada scandens* from South America by ocean currents, which frequently deposit them along the west European seaboard in a viable condition.

**The Social Life of Plants (Synecology).**—The foregoing considerations lead naturally to the conception of definite communities of plants, and it is the study of these social groupings which is the particular domain of *synecology*. The largest groupings that can be recognized are related to the broad climatic features of the earth's surface; such are termed *formations* and are well represented by the tropical *rain forest*, a community characteristic of areas within the tropics with high and continuous rainfall, consisting of a luxurious vegetation in which there are a great variety of broad-leaved evergreen trees, numerous woody climbers (*lianes*), and epiphytic plants, the whole presenting a great complexity of structure. Other examples of formations are the deciduous forests of temperate regions, the grassland formations of the American prairies and the African veld, or the deserts of arctic and tropical regions. These formations can be further subdivided, according to the species which play the major rôle in the plant community, into *associations*, where several species take a leading rôle, or *consociations*, where there is one predominant species. Since even in these the subordinate species vary from one part to another, *societies* within the association can be recognized.

The deciduous forest formation of America presents in Indiana and Missouri associations in which oak and hickory are the chief features, whilst in the region of the great lakes it is represented by an association of birch and maple. In central Europe the same formation is represented by the very mixed forests of beech, hornbeam oak, etc., of the Danube region, by the Mediterranean chestnut forests, by the oak forests of Austria and other types. In Britain consociations are the rule, each characterized by a single dominant tree and associated with particular soil conditions. Thus the ashwoods are chiefly found on limestone soils, where the conditions are moist; beechwoods on dry soils, particularly those derived from chalk; birchwoods constitute the uppermost zone of woodland in mountain districts and also occur as a temporary phase on felled areas; alderwoods occupy the wettest soils; oakwoods of *Quercus Robur* are a feature of the moister and more fertile clays and loams, and oakwoods of *Q. sessiliflora* of the less fertile, acid, and usually drier non-calcareous soils, especially on the valley slopes of the west. Within an English oakwood some areas are covered with a carpet of *Mercurialis perennis* and *Scilla nutans*, others with *Anemone nemorosa* or *Ficaria verna*, furnishing examples of societies within the consociation. Such illustrations serve to indicate the use of these synecological terms; but for an account of the plant communities of the world the reader is referred to the works cited on p. 18.

Every plant community has something of the attributes of an organic unit, in that it possesses a more or less definite structure and has a life history in which juvenile, adult, and senile phases

can be recognized. The structural organization is well illustrated in the temperate deciduous woodland, where three definite strata are usually present, respectively consisting of trees, shrubs and herbs, whilst beneath the lowest tier or ground flora there is often a carpet of mosses and the surface soil is rich in fungi and bacteria. Although less conspicuous, these flowerless plants are just as important a part of the community and have as definite a floristic composition. Beneath the surface the root systems of the higher plants exhibit a stratification comparable to that of the aerial organs, and the differing depths to which the roots of different species penetrate, as also the different periods at which they make their maximum demands on the food supply in the soil solution, are features which tend to reduce the competition between species and render possible that dense intermingling which results in the succession of seasonal changes. It must, however, be realized that the architecture of any community necessarily connotes different conditions in its various parts so that the environment occupied for example by the ground flora of a tropical or temperate forest, or by the lowest stratum of a fen is markedly different, as to humidity and illumination, from that of the tree layer in the one or the tall reeds in the other.

The different associations in a plant formation show an analogous structure often built up by very diverse species, and no better example of this could be furnished than by the desert vegetation of Texas and Mexico, characterized by succulent Cactaceae, and that of Africa, characterized by succulent Euphorbiaceae. Some of the members of these totally unrelated groups are so similar when not in flower as to be most readily distinguished by wounding, since the euphorbias possess milky juice which the cacti do not. Each association is distinguished by the presence and relative abundance of certain species and the absence of others. Those which are almost invariably present in a community are termed *constants*, but their diagnostic value is often low owing to their constancy in more than one association. Examples are furnished by *Mercurialis perennis* in the beechwoods of Britain and *Viola sylvestris* in the oakwoods. Of greater significance are the *characteristic* species which occur more or less exclusively in a particular community, as *Hordeum sylvaticum* and *Monotropa hypopitys* in the beechwoods of Britain or *Psamma arenaria* on European sand-dunes. Such characteristic species may be at the same time constants but are often of local occurrence. Many of the subordinate or accessory species are found in a variety of communities but have their characteristic frequency in each.

**Succession.**—Careful observation shows that, quite apart from the periodic rhythm of the seasonal changes, no community is stable. The physical environment itself is slowly altering, partly as a consequence of climatic action, partly through the influence of the living covering. Commonly, these changes are too secular in character to be readily appreciated, and it is only where the alterations in the physical environment are unusually rapid that the existence of a definite life-history in the plant community can be easily observed. In general, the tendency is for communities characterized by extreme conditions, as of dryness or wetness, to approach the mean. The process is well illustrated by the formation of sand-dunes, where the early stages consist of sandy accumulations around plants of marram grass (*Psamma*) or other pioneer species; these by their continued growth, as fresh layers of sand are added, not only stabilize the sand but by the decay of their older parts add organic material and so materially increase the water-retaining capacity of the soil. With the consequent amelioration of the extreme desert conditions species less specialized than the first colonizers can become established, and so there is a cumulative increase in the stability and quality of the habitat. The original dune-units increase in size and coalesce, so that the "yellow dune" gives place to the "grey dune," carpeted with continuous vegetation, and ultimately comes to bear scrub or even forest. Similarly the first occupation of the submerged mud in some estuary by almost microscopic seaweeds is the vanguard of a sequence of plants which progressively raise the level of a salt-marsh till it becomes pasture often of high economic value. The zones of vegetation which can be seen bordering the margin of a shallow lake present a sequence in space from within out-



wards which corresponds closely with the sequence of changes in time which led to the present condition of the outermost. Another familiar example is the passage of enclosed pasture to scrub and finally woodland. In such *successions*, as these sequences are termed, each phase is distinguished by the presence of certain species, and the number and size of these tends usually to increase as the succession proceeds. Frequently in the final stages, however, one or two species again come to predominate, and since these often determine the physiognomy of the community they are frequently referred to as the *dominants*. Successions have been extensively studied by American ecologists and F. E. Clements has utilized this aspect as the basis for a classification of plant communities.

**Competition.**—Except perhaps in the so-called “open” communities such as those of deserts, where the individual plants are separated by bare soil, there is probably always direct competition between the constituent members. The conditions of the habitat exert a selective action, stimulating the development of certain species and depressing the vigour of others. If protected from competition many species can grow in habitats where they do not occur naturally. Many aquatics can survive under terrestrial conditions, and a large proportion of alpine succeed under cultivation in the lowlands. It is thus commonly not a question of whether or not a species can grow, but whether it can grow well, and competition often resolves itself into a capacity to obtain the requisite share of such essentials as light, air, water and mineral salts. In competition for light the naturally taller species is at an advantage; it can grow above and shade its competitor. Thus, wherever soil and climate can support forest vegetation, this tends to be the end phase or “climax” in the succession. So, too, trees which cast a deep shade are usually successful in competition with those having a light canopy. The birch, which by reason of its light wind-born fruits readily colonizes denuded woodland areas, eventually gives place to trees of heavier canopy such as the oak. Large size, however, is usually associated with delay in reproductive activity and the prolonged life-history renders the arboreal habit less successful than the herbaceous under the stress of conditions imposed by the presence of man. This is reflected in the steady diminution of the area occupied by natural forests.

Almost any feature in the organization or life-history of the individual which fits it for its particular habitat is at the same time a passive agent in its survival; but amongst the features which may be regarded as of importance in aggressive competition may be mentioned especially the rate of vegetative spread, the annual output of seeds, the efficiency of the mechanism of dispersal, and the extent and character of the root and shoot systems.

**Economic Aspects.**—Finally, mention should be made of the importance of the study of plant communities and their successions for the proper control and exploitation of forests and the maintenance of high yielding pastures. The naturally occurring species of an area serve as a valuable guide to agricultural practice, since their presence is in effect a product of the complex built up of soil and climate. A study of the natural relations of species is, moreover, a useful guide to their artificial juxtaposition in the practice of agriculture, forestry and horticulture (*qq.v.*).

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## PHYSIOLOGY OF PLANTS

The physiology of plants deals with the functions of the living plant as morphology and anatomy deal with form and structure. Physiology aims to explain the functions of an organism in terms of physical and chemical processes. Physiology thus considers the living organism solely from the mechanistic standpoint, *i.e.*, from the standpoint that the organism is a machine albeit a very complex one. In this attempt to explain the organism in the terms of a machine the physiologist is supported by the fact that the organism appears to obey so-called physical laws in much the same way as does dead material. The living organism for example obeys the law of the conservation of energy, the amount of energy given out by the organism being equal to the amount taken in in food; again the plant or animal conforms also to the second law of thermodynamics which relates to the use of free energy.

**Characteristics of Living Organisms.**—Although it is impossible to give an exact definition of a living organism some of its characteristics may be pointed out. Whether one is dealing with a plant or animal of a single cell, or of a large organism such as an elephant or a tall tree, it is evident that it is a machine constructed to carry on certain processes, such as the absorption or building up of food; the process of respiration (*see below*) and the processes of growth and reproduction. One great difference between the living machine and any other machine is that the living machine is infinitely more complex than any man-made machine. Then again the processes going on in the organism are not independent of one another but are to a high degree, what is called, *integrated*. All the processes are interlinked or related, the finished material of one process being often the raw material of the next, and all being so closely associated as to lead to movement or growth or reproduction or some other activity of the organism. Another marked characteristic of the living machine which distinguishes it from all other machines is its power, to put it colloquially, to build itself up as it goes along. In other words the growing organism is a functioning unit which adds to itself and increases the size of the machine by its own functional activity. Another characteristic of the plant or animal is its constant reaction to the environment and its constant adaptation to changes in the environment. It is true that a carefully dried seed kept at a low temperature may appear to be quite inert, though still alive as is shown by its power of germination under suitable conditions; yet all active organisms show a constant interchange with their environment. Even in the case of the seed it is probable that some interchange, such as respiration, is still going on though at such a slow rate that our present methods of analysis are too coarse to recognize it. Another characteristic of the organism is that any apparent steady state or equilibrium is not a *static* but a *dynamic* one. If the normal organism appears to be in an inactive state it is simply that the constructive processes just balance the destructive processes, not that the processes are at a standstill. The living organism is like a battery which is constantly running down and requires constant recharging, though the recharging goes on at the same time as the discharging. The majority of cells require oxygen for their mere continued existence even in a resting condition and additional oxygen when in a state of activity. This need of oxygen even during quiescence indicates that a quiescent state of the cell is only an apparent quiescence, a state of dynamic not static equilibrium. Again the giving out of heat by all living organisms even when apparently inactive indicates the dynamic equilibrium of chemical processes going on in the cells. These exceedingly intricate processes continue unceasingly throughout the life-period of every cell in the simplest as well as in the most complex organisms.

**Organization of Cell.**—All living cells contain, or consist of, a viscous, glairy material (somewhat akin in consistence to un-boiled white of egg) known as protoplasm. Protoplasm is not of course a single substance but a very complex system; it has been described as the “physical basis of life” since life as far as we know, does not appear to exist apart from protoplasm. An analysis of an active plant tissue, like lettuce or beet leaves, shows that it contains about 90% water. Of the *dry* material we should



find carbon 38.19%, hydrogen 5.1%, oxygen 30.8%, nitrogen 4.5% and ash 21.5%. Similar results would be found for most plant material in the dry state though resting materials such as the potato tuber and the wheat grain would have only 2-4% of ash. Active protoplasm, and living material generally, is characterised by a high percentage of carbon owing to the large amount of organic matter, and in plants by a high percentage of oxygen owing to the large amount of oxygen-rich materials as carbohydrates (sugars, starch). A small proportion of nitrogen is also always present in living material. In ordinary analyses of plant material the protoplasm is only a small proportion of the material, a large proportion is dead cell-wall material, the contents of the cell vacuole (*see above, Cytology*), and protoplasmic inclusions. The nearest approach to an analysis of protoplasm is that which has been made of certain myxomycetes (*see FUNGI*) which exist as naked masses of protoplasm. Kiesel (1925) has examined *Reticularia lycoperdon*. He finds in a hundred parts of the dry weight:—protein, 29.1, other nitrogenous substances, 12.0, nucleic acid, 3.7, oil 19.1, carbohydrates generally 9.9, glycogen 15.2, also lecithin and cholesterol. This analysis is of course very incomplete; 6% of the material was not determined and a large number of substances present in small quantities only must have been overlooked. We note, however, the large amount of protein and this is a general phenomenon; just as we find life associated with protoplasm so we find protoplasm associated with protein.

It is clear that protoplasm must be a material, or rather a system of materials of very special nature since the enormous number of chemical reactions associated with life processes go on within it, and are apparently controlled and brought by it into proper co-ordination. Protoplasm also is concerned with the hereditary process, with the handing on to the male and female cells and from cell to cell in the body of the plant or animal, of the special qualities which cause the offspring to resemble their parents. (*See CYTOLOGY.*)

The modern theory of the special peculiarities of protoplasm associated with its life activities may be termed the *physico-chemical theory*. In this view stress is laid not so much on any special organization of the protoplasm as on its peculiar physico-chemical condition.

It is pointed out that proteins are colloidal in nature or rather exist in the colloidal state (*see COLLOIDS*) and that, on one hand, many of the peculiarities which distinguish chemical processes in the living organism from the same processes occurring in the laboratory, and the peculiar co-ordination of processes which marks the living cell—and indeed of the whole organism for the harmony of the working of the plant or animal body is a commonplace—are related in some way with the colloidal nature of the protoplasmic substratum in which they occur. It cannot be said, however, that the colloidal theory carries us very far. We know that material in the colloidal state exhibits an enormous extension of surface and that substances may accumulate on this extended surface (by a process known as *adsorption*) and react together at a much faster rate than would otherwise be the case. The theory, however, does not explain how the numerous chemical processes going on in the cell are on the one hand kept from interfering with one another, and yet on the other hand are brought into close interrelationship and co-ordination. Still less can a colloidal theory explain the even more complicated processes of *growth*, of *differentiation* (the development of new and different parts as the plant or animal develops), and of heredity. It is clear also that the protoplasm is not a simple colloid of two phases, such as are found in gamboge in water where the particles of gamboge are the one phase and the water surrounding them the other phase. In the protoplasm there is not only protein material but oily material (so-called lipin material) appears to be essential and probably also carbohydrates play a part. We know furthermore, that various salts (of potassium, calcium, etc.) are necessary. The physical relationship of the colloidal protoplasm must therefore be far more complex than that of any colloidal material studied in the laboratory. Any attempt to explain the peculiar relationship of the processes occurring in living organisms by reference to the behaviour of a complicated, dead, colloidal

medium is largely speculation since the behaviour of such a medium is unknown.

**Enzymes.**—When dealing with the colloidal organization of the cell reference must be made here to the substances known as enzymes (*q.v.*). These are substances of unknown nature which can be extracted from dead cells whether plant or animal, and they must certainly play a very large part in the chemical processes going on in the living cell. They have three marked characteristics; they can act as catalytic agents, *i.e.*, they cause many chemical processes to go on at a much faster rate than would otherwise be the case; in chemical language they accelerate; they can thus cause rapid changes to occur which in their absence require a high temperature or the action of strong acids or alkalis. Secondly they act in very minute quantities and do not themselves appear to be used up in the process which they accelerate, for example invertase can break down 1,000,000 times its weight of cane sugar. Thus they partake of the nature of chemical catalysts. Thirdly they are usually sensitive to heat (thermolabile) their activity being usually destroyed by temperatures well below that of boiling water. It is to be noted that the processes they accelerate may be either breaking down processes or building up (synthetic) ones, and that they can accelerate both such processes. Enzymes have been very actively investigated of late years especially by Willstätter and his pupils, but their nature is still obscure. They seem to be a part of the mechanism of the living cell by which the rate of various chemical processes are controlled. These enzymes seem to be of colloidal nature, or to have a colloidal carrier, though apparently they are not of protein nature; and furthermore their action is markedly *specific*, that is, the enzyme which affects the rate of one chemical process is unable to affect the rate of another process of marked chemical similarity. For example, sugars closely related in chemical composition require different enzymes to bring about changes in them. This is one of the puzzling aspects of cell physiology for it seems difficult to believe that the cell has a battery of enzymes to carry on the very numerous chemical processes with which it is concerned. Enzymes can, of course, only be studied outside the cell and it may be that the conditions in the living cell are different.

In relation to the cell organization it must be pointed out that many of the processes going on in the cell are *balanced or reversible reactions*, that is reactions which are capable of going in either direction; a good example of this is the formation of fats. These substances consist of glycerol (glycerin) combined with a fatty acid. In the presence of a special enzyme, lipase (found in castor oil seeds and in the animal body), this reaction is capable of going either way, the fat may be split up into glycerol and acid, or the acid and glycerol may be combined to form fat; the lipase accelerates *both* these processes. Whether the reaction goes in the direction of synthesis or analysis depends not on the lipase but on the concentration of the substances taking part, *i.e.*, fat, glycerol, fatty acid and water. It is probable that by controlling the amount of water available for particular reactions the cell is able to control the direction in which such a reversible process shall go.

## WATER RELATIONS OF THE PLANT

It is well known that water is essential for all life processes. A seed may be thoroughly dried and still be capable of germination but it is in a dormant state; for its germination and ordinary activities water is necessary. It seems essential that the colloids of the protoplasm should be swollen (imbibed) with water in order that it may be active. Furthermore all the chemical processes of the cell go on in a watery medium and water is necessary for the solution and reaction of the substances concerned. The more active tissues of the plant generally contain particularly large quantities of water as was seen in the case of the green leaf; in the older and less active parts the percentage of water is less because many of the cells have been reduced to dead husks of cell wall material.

## WATER RELATIONS OF THE CELL

As is shown above, under the heading of *Cytology*, the mature



cell consists of a cell-wall lined inside with a thin layer of protoplasm, which itself encloses a central space, the *vacuole*, filled with cell sap. (See above, *Cytology*.) The sap contains various dissolved substances, sugars, nitrogenous materials, a variety of inorganic salts and other substances which are sometimes of colloidal nature. Curiously enough the majority of the substances are highly soluble in water and yet if a slice of beetroot is placed in water the amount of material passing out from the sap of the living cells is comparatively small as long as the cells remain alive; the cells on the other hand are capable of taking up water. We have then a peculiar condition of affairs in which water can enter the cell but the passage out of soluble substances present inside the cell is hindered. This effect is due, not to the cell wall which appears on the whole to be dead and inert, but to the living layer of protoplasm which is often known as the *plasma membrane*. This exhibits when living a condition of *semipermeability* since it lets water readily pass in and out, but hinders the passage of certain dissolved substances such as those in the sap. Water is attracted into the cell by the dissolved substances inside just as it would be into a sugar solution enclosed within a pig's bladder, which also roughly is semipermeable allowing water to enter freely but being more or less impermeable to the sugar. As a result of the entry of water the cell becomes swollen up and turgid and exerts what is known as *osmotic pressure* on the elastic cell wall or membrane which is thus stretched. Whole tissues of the plant are thus given a rigidity which is not due to their actual mechanical strength. The dependence of this rigidity on plentiful supplies of water is well seen in the case of leaves and the stems of herbaceous plants which often wilt, *i.e.*, become soft and flaccid, on a hot summer's day. Directly so much water is lost that the wall is no longer expanded, the rigidity of the cell must completely disappear.

**Plasmolysis.**—That the cell allows water to pass both ways and that the plasma membrane hinders not only the exit but also the entry of various substances into the cell is shown by the action on the living cell of a solution of cane sugar or of some salt such as potassium nitrate, or calcium chloride. If the living cell is placed in a solution of one of these substances of a concentration greater than that of the cell sap, water is drawn out of the cell and the cell collapses; this process is known as plasmolysis. It gives a convenient method of measuring the osmotic pressure of the cell. We find that concentration of cane sugar which brings about what is called "incipient plasmolysis," that is, the stage at which the plasma membrane has just begun to be withdrawn from the cell wall at one point. In this condition the osmotic pressure inside and outside the cell must be the same and since the osmotic pressure of the sugar solution can be determined the pressure of the cell sap is known. Osmotic pressure is generally expressed in terms of atmospheres; if a cell has an osmotic pressure of 5 atmospheres, the pressure exerted on a given area of the cell wall is five times as great as the downward pressure exerted by the atmosphere on the same area, which is about fourteen pounds to the square inch. Pressures of 5 to 40 atmospheres are common in plant cells and those of the order of 150 atmospheres have been observed. These pressures seem large but owing to the very small size of the cell the actual forces concerned are small.

#### **Osmotic Pressure, Turgor Pressure and Suction Pressure.**

—When a cell is supplied with water it goes on absorbing and at the same time expanding with the result that the *backward* pressure of the stretched and elastic cell wall becomes greater and greater, until finally it equals the osmotic pressure of the cell contents; this backward pressure of the cell wall is known as *turgor pressure*. The cell is then fully expanded and fully imbibed and can absorb no more water. If on the other hand the cell is not fully imbibed the osmotic pressure is greater than the turgor pressure and the cell will tend to suck or draw water into the cell. When the cell is flaccid, as in the plasmolysed condition, there is no turgor pressure. It is clear that the difference between the osmotic pressure and the turgor pressure measures the pull with which the water is drawn into the cell; this difference is known as *suction pressure*. The term water absorbing power is sometimes employed but the first is by far the more satisfactory

term since we are dealing with a pressure and not a power. If  $P$  = the osmotic pressure of the cell sap,  $T$  = the turgor pressure, and  $S$  the suction pressure, then  $P - T = S$ . We see then that the suction pressure is that fraction, if any, of the osmotic pressure left over from balancing the turgor pressure (backward pressure of the wall). When the cell is fully imbibed with water then  $P = T$  and so  $P - T = 0$  and there is no suction pressure. When the cell is flaccid  $T = 0$  and therefore  $P = S$ , *i.e.*, the suction pressure is equal to the full osmotic pressure.

As the suction pressure is such an important quantity the question arises as to its measurement. As it represents the pressure with which water is drawn into cell from outside it is evident that if we just balance this pressure inside the cell by an equal pressure outside, the cell will neither take in nor give out water, and therefore will neither expand nor contract, *i.e.*, will remain unaltered in volume. This consideration is the basis of the method of measurement. The cell, the suction pressure of which is to be determined, is placed in purified paraffin oil under the microscope and its volume measured; this gives its normal volume since it does not absorb the oil nor does it lose water while immersed in the oil. The cell is then removed and placed in various strengths of cane sugar solution or some other plasmolysing agent until a concentration is found at which the volume is the same as measured in the oil. If the cell does not change in volume while lying in a watery solution it must be that its suction pressure is opposed by an equal pressure in the opposite direction. This counter pressure must be the osmotic pressure of the cane sugar solution which just keeps the cell at its original volume. The osmotic pressure of this solution thus gives the suction pressure of the cell in the state in which it was investigated; like the osmotic pressure it is usually expressed in atmospheres.

#### **ABSORPTION OF WATER BY THE PLANT BODY**

Water plants are surrounded by a very dilute solution of salts, as in the case of fresh water or a somewhat stronger solution in the case of sea water. Being surrounded by a watery medium the loss of water, and accordingly the need for absorption of water, does not play any very large part in their economy. The conditions are very different with land plants which, in the case of higher plants, often expose very large surfaces to the air and consequently lose great quantities of water in the form of vapour, which passes through the pores in their leaves in the process of *transpiration* (see below). Such land plants must therefore take up larger quantities of water from the soil and the rate at which they can take up water will depend upon the forces with which the water is held in the soil for it is these forces which the *suction pressure* of the cells in contact with the soil have to overcome.

**Soil Conditions.**—The soil is a very complex material consisting of (a) mineral particles of various sizes and varied chemical composition, (b) of organic matter usually in the form of a dark brown material known as *humus* which is derived for the most part from the decomposition of remains of dead plants which formerly grew upon the soil, (c) water, which is held by colloidal adsorption in films on the mineral and humus particles and also, to a certain extent, within spaces of the soil, (d) air which is found in the spaces between the soil particles. The air can, of course, be displaced by water, as in the case of a water-logged soil where all the pore spaces of the soil are filled with water. Soils differ very much in what is called their *mechanical* composition, *i.e.*, in the relative amount of particles of large and small size. A sandy soil has a large proportion of large particles, a clay soil has a large proportion of small particles, and to this is due their great difference in behaviour both in relation to water-retention and their response to mechanical treatment (*e.g.*, ploughing) and to fertilizers. The relation of size of soil particles to the water holding power of the soil is particularly important in reference to the physiology of the water absorption of the plant from the soil, and attempts have been made to estimate the relative forces with which the water is held by different soil constituents. Briggs and McLane working in America determined the amount of water held back by various soils when they were whirled round with enormous rapidity in a centrifuge;



the centrifugal force resulting from the rapid rotation at first causes water to be thrown off but it is finally balanced by the water retaining forces of the soil particles. By comparing the behaviour of a number of different soils of different compositions they deduced that if the water holding capacity (moisture equivalent) of the particles of size 2.0 to 0.05 mm. diam. (*i.e.*, coarse and fine sand) be taken as unity, the corresponding equivalent for the particles of below 0.05 to 0.005 mm. diam. (silt) is 12, while that for the particles of less than 0.005 mm. (*i.e.*, clay) is 57. The silt is partly colloidal, and the clay highly colloidal, and the high water-holding power is due to the colloidal properties. The humus also is of colloidal nature and of marked water-retaining power and its capacity in that respect may be taken as about the same as that of the colloidal clay. The forces with which the water is held in different soils and in the same soil with different amounts of water has been investigated by Shull by what may be termed a biological method. It is well known that dry seeds will take up water actively and often with considerable force, the amount they can take up depends upon the force with which the water is held in the medium from which it is being taken. The method consists then in placing dry seeds in different soils with different content and determining the amount of water taken up after a given period, say 48 hours. Similar seeds are then placed at the same temperature, (a) in concentrated solutions of lithium chloride and sodium chloride of high osmotic pressure, or (b) over sulphuric acid of different concentrations. If the seed takes up in the same time the same amount of water from a given soil as from the salt solution or from the moist air over sulphuric acid the water retaining power of the materials in which the seed is placed should be the same. Now the osmotic pressures of the solutions—which represent the forces against which the water-absorbing forces of the seeds are acting—are known and so the water holding power of the soil can be expressed in atmospheres. The results show that the water absorbing power of the seeds is very high, for they will take water from a saturated solution of lithium chloride which has an osmotic pressure of nearly a thousand atmospheres. They show also, as was to be expected, that in an ordinary loam soil the forces with which the water is held go up markedly as the water becomes reduced in amount. In a silty loam investigated the forces holding water were negligible when there was 20% of water in the soil, but when it was reduced to 15% the forces were several hundred atmospheres and when reduced to about 10% of the order of 1,000 atmospheres pressure. With sand the condition is very different for the material is non-colloidal and the water is only loosely held; only when the water content is reduced to a very small amount does the pressure become considerable.

**Dynamic Relations of Water Absorption.**—The observations which have been described above only gives us a picture of static equilibrium between the plant and the soil. They show what the conditions are when there is a balance between the forces pulling water into the seed (or root of the plant) and the forces holding the water in the soil, that is they show us the condition when water is no longer taken up. This, however, though helpful, as giving some measure of the forces which the root has to overcome, gives us a very imperfect picture of the relationship to the plant. The plant is continually giving off water in the process of transpiration and unless the rate of absorption keeps pace with the rate of loss of water the water content of the plant will begin to fall. The plant will flag when this difference in the two rates has existed for a short period and the plant will be dead long before the rate of absorption has fallen to zero. The equilibrium between absorption on the one hand and loss of water by transpiration on the other is thus, like the equilibrium in the living cell, a *dynamic* not a static one.

### TRANSPIRATION

The term transpiration is applied to the process of loss of water vapour from the aerial part of a land plant; it is of the nature of controlled evaporation. The transpiratory losses take place mainly from the leaf surface since these organs expose a large surface for evaporation and are supplied on the epidermal surface with pores

known botanically as stomata. (*See above, Anatomy.*) These pores interrupt the otherwise continuous layer of *cuticle* which covers the surface. In its absence the loss of water from the leaf surface would be very large and uncontrollable. The cuticle is, however, not completely waterproof so that we can distinguish *cuticular* transpiration and *stomatal* transpiration. The second is very much the larger, being usually 80–97% of the whole, though under special conditions, as in a tropical rain forest, the cuticular transpiration may be as high as the stomatal.

**Measurement of Transpiration.**—That transpiration occurs can be shown by the loss of weight of a potted plant, when the pot and surface of the soil are protected from water-loss by rubber sheeting; this gives a convenient method for measuring the rate of transpiration. It is not applicable to plants growing in the ground; for such plants paper dipped in a cobalt chloride solution, dried and applied to the leaf may be employed. On the absorption of the water vapour coming from the leaf the colour of the cobalt chloride paper changes from pink to blue, and the rate of this change gives some measure of the rate of transpiration.

**Size and Arrangement of Stomata.**—The stomata are more commonly confined to the lower surface of the leaf—the cuticle on the upper surface being then continuous, though leaves with stomata on both sides frequently occur. The stomata are very small pores, those of the sunflower leaf being about  $\frac{1}{100}$  of a millimeter (*i.e.*, about  $\frac{1}{2500}$  of an in.) in diameter. They are very numerous, varying from 40 to 300 per square mm.; a sunflower leaf may thus bear 13,000,000 of them. The pore is bounded by two special cells known as *guard cells* (as described in the anatomy of plants) and open below into a chamber which is bounded by the walls of the green cells (*mesophyll*) of the leaf. These cells are full of water and from their wet cell walls water naturally evaporates into the space, and by the physical process of gaseous diffusion passes out of the stomatal pore into the drier air outside. As the stomata occupy a very small proportion of the total surface it might be supposed that the rate of passage of a gas or vapour out or in would be very slow. It was shown, however, by Brown and Escombe in 1900 that such very small pores allow of a much greater rate of diffusion than might be expected. It is found that provided the pores are not too close to one another the rate of diffusion is proportional to their diameter and not to their area.

**Effect of Various Conditions on the Rate of Transpiration.**—Transpiration like most physiological processes is markedly affected by external conditions. Since the process is essentially one of evaporation, one of the most important factors (the term factor is applied to a particular condition affecting the rate of a process) is the humidity or relative dryness of the air to which the plant is exposed. The drier the air the more rapid, on purely physical grounds, will be the rate of diffusion of the water vapour through the stomatal pore. This is due to the big difference of the water content (humidity) of the air below and above the pore. The proper measure of the evaporating power of the air is not the actual relative humidity (or percentage saturation of the air) but the *saturation deficit* and this is markedly affected by temperature. Air 70% saturated at 10° C has only about half the saturation deficit of air 70% saturated at 20° C, and so its evaporating power is only half. Temperature itself has very little effect on transpiration or evaporation except in so far as it affects the evaporating power of the air. Atmospheric pressure has only a slight effect since evaporation tends to go up with a fall in barometric pressure but it is so small that it can under ordinary conditions be neglected. Wind is a very important factor in transpiration. It is well known that plants suffer very much in windy situations and “wind-breaks” are often put up for plant protection. The ill effect is mainly due to the enhanced rate of transpiration, which is the direct physical effect of the removal by the wind of the layers of air in contact with the leaf.

**Effect of Light.**—If the rate of transpiration is measured, say by weighing a potted plant under appropriate conditions, it is found that the water loss is much greater by day than by night and this occurs even if the evaporating power of the air and the temperature are kept constant. It is a well known effect of light



upon the higher terrestrial plants. This effect occurs in an ordinary diffused light so it cannot be due to the heating effect of the rays, for in such circumstances such effect is practically negligible. The effect produced by the light must be due to some change in the leaf itself since the factors affecting evaporation have remained unaltered. As the transpiratory water loss is through the stomata we should expect some change in the size of the pore, and it is found that in the majority of leaves light causes a widening of the stomatal pore and darkness a partial closure.

**Stomatal Action.**—As already stated the stomatal pore is bounded by two guard cells and it is by changes in their shape that the alteration of the pore is brought about. Their shape, the relative thickness of their inner and outer walls, and their attachment to the epidermal cells are such that when they become more turgid their inner walls—those facing the pore—move apart and so the pore widens, while on a reduction of turgor these walls approach one another and the pore becomes less in size. When the cells become collapsed, as in drying or by plasmolytic agents, the size of the pore is very much reduced though probably not to zero.

The mechanism by which light brings about alterations of turgor in the guard cells has been much disputed. It has often been held that the stomata open in light owing to the increased turgor due to the accumulation of sugars produced by the assimilatory activity of the chloroplasts of the guard cells. This view is quite untenable for the guard cells open in the light in the absence of external supplies of carbon dioxide. Lloyd (1908) also has shown that guard cells containing only leucoplasts behave similarly to normal ones. It was shown also by the same observer that the guard cells in the early morning, when the pore is closed, show much starch, which disappears during the day to reappear again in the evening when the stoma closes. This led to the view that the light affected the starch-sugar ratio in the guard cells. In the day insoluble starch would change into soluble sugar and the turgor of the cell rise, in the night the sugar would change back to starch and the turgor fall. The turgor changes would bring about the corresponding changes in the size of the stomatal pore. This view received support from the observations of the osmotic pressure of guard cells. In *Rumex patientia*, for example, it was found that the osmotic pressure of the guard cells is 23 atmospheres when they are fully open, about midday, while only 13–14 atmospheres when the pore is closed at night. It is found that in addition to light other factors such as neutral salts and acids and alkalis affect the starch-sugar relation and so stomatal movement. This is rather what might be expected since the change from starch to sugar and the reverse is almost certainly an enzymic one. Further work by G. W. Scarth in 1926 indicate that acetic acid and ammonia, *i.e.*, both acid and alkali, will cause the opening of the stomata; in an intermediate range where there is slight acidity the guard cells remain closed. This suggests that what the guard cells respond to is a change in the concentration of free hydrogen ions (*i.e.*, the free hydrogen parts of the acid molecule when it is dissociated in water) of the solution. In this view light affects the “acidity” of the leaf as a whole either by altering the content of organic acids in the cells, or the concentration of carbonic acid by affecting the rate of assimilation. There are indications that the effect is more complex and that the change in the starch-sugar ratio is too slow to explain the rapid turgor changes that occur. It is probable that there is present in the cell sap of the guard cells some colloidal material which absorbs water and that the amount of water the colloid takes up is altered by changes in the concentration of the hydrogen ions of the cell.

**Control of Transpiration by Stomata.**—The question of the control of the rate of transpiration by the stomata has also been much debated. The older view was that the opening and closing of these pores had an important controlling effect. This view was abruptly called in question by Lloyd in 1908 who denied the regulation of water loss of leaves through stomatal closure. It is clear from later work that the stomatal aperture may vary widely while the rate of transpiration shows no corresponding change; thus the stomata may go on opening in the middle of the day while

the transpiration rate falls. The matter is again complicated by the fact that the rate of loss of water vapour by the stomata is also affected by the accumulation of moist layers of air upon the surface of the leaf. If the stomata open more widely when such layers are present there may be little possibility of any faster diffusion of water vapour through the pores. Calculations indicate that in still air the layers of moist air on the leaf exert the most effect, and it is only when the stomatal pores have become very narrow that the pores can have a controlling action. In wind, however, these moist layers are removed and the stomatal pore can exert a controlling action at any degree of opening. It must be borne in mind however that the stomata are very sensitive to light but their response to losses of water by the leaf are slow, so that they cannot keep the water content of the leaf constant by controlling the stomatal pore.

**Direct Action of Light on Leaf Cells.**—As already described light markedly increases transpiration by causing the stomata to open, but the question arises as to any possible direct effect on the mesophyll. It was claimed by Francis Darwin (1914) that in a leaf which had been vaselined on both sides, to block the stomata, and then slit so that the mesophyll cells transpired directly into air, light still increased the rate of water loss by as much as 36% in the case of the leaf of ivy. Such a huge increase seemed very unlikely, so the matter was again investigated by Henderson (1926), who showed that, when all allowances were made for possible changes of temperature, light did produce an increased rate of evaporation from the mesophyll cells of the leaf to the extent of about 5%. The exact mechanism of this is obscure; it is probably some effect on the resistance of the protoplasm to the passage of water through it to the surface of the cell. In the light the cell wall would be more fully imbibed, *i.e.*, wetter than in the dark.

**Advantages and Disadvantages of Transpiration.**—This question is often debated, the extreme positions being (1) that the process is an *unavoidable evil*, (2) that it is a *physiological necessity*. The idea of its physiological necessity is mainly based on the view that the water and the inorganic salts that the plant requires are taken in together in the form of the very weak solution which occurs in the soil, and that the excess water must be got rid of in transpiration. This view is based on the erroneous assumption that water and salts enter the plant together. As a matter of fact the forces bringing about the entry of water and the entry of dissolved salts into the root cells are of an entirely different nature; the two must enter quite independently. Whether transpiration is an “evil” may be debated but it is perfectly clear that given the necessity of taking in gases from the air, the loss of water by plants is quite unavoidable. The same pores which allow the entry of gases must also allow of the passage out of water vapour. The plant could only stop such water loss by having a continuous cuticle, and then the supply of carbon dioxide for the manufacture of sugar and starch would almost completely be cut off. *The loss of water by transpiration is a necessary result of the construction of the plant.* It has been suggested that a rapid stream of water rising in the wood (*see below*) is necessary to convey the salts to the leaves, but it is found that a reduction of transpiration does not necessarily reduce the accumulation of salts in plants. It may be that some *minimum* rate of upward water flow is necessary to transport the salts to the higher parts of the plant. Transpiration may also play some small part in keeping down the temperature of plants exposed to the direct rays of the sun.

### MOVEMENT OF WATER IN THE PLANT BODY

The water that enters the plant from the soil ultimately escapes from the leaf surface passing through the stomatal pores in the form of water vapour. The question arises as to the path taken by this water. It has been known a long time that the main body of the water passing through the vascular plants travels by way of the xylem, *i.e.*, the wood. (*See above, Anatomy.*) The evidence for this is various. It is found that if the trunk of a tree is “ringed,” *i.e.*, cut through right down to the wood throughout the circumference of the tree, water continues to pass up the tree for a long time



and apparently unhindered. Again if cut shoots are placed in a solution of a dye such as eosin, the wood alone is deeply stained showing that the dye solution has travelled up through this tissue. The frequent occurrence in the wood of wide open tubes containing no protoplasm also indicate its function as a conducting channel.

**Passage of Water Across the Root.**—The root as anatomical studies show, usually exhibits elongated outgrowths from certain of its superficial cells. These outgrowths are known as *root-hairs* and serve to increase the surface of the root available for absorption. These hairs are in contact with the films of water on the soil particles and they can withdraw water from the soil if their suction pressure (*see above*) is greater than the imbibition forces of the soil, *i.e.*, the forces tending to retain the water in the soil. The water thus absorbed, if it is to reach the leaves, must pass across the root to the xylem strands and the question arises as to the mechanism of this transport. It has been shown by the work of Ursprung and Blum that there is a *gradient of increasing pressure* from the root hair to the endodermis; by this means the water will pass from cell to cell across the cortex. At the endodermis there appears to be some abnormal condition for in the absorbing root of the broad bean it is found that while the suction pressure rises from outside to the sixth cortical cell from 0.7 to 3.0 atmospheres, yet at the endodermis it falls to 1.7 atmospheres; as a result the direction of movement of the water should be reversed and the water pass back again; this cannot be the case so the matter requires further investigation.

**Ascent of Water in the Wood.**—That the water rises in the wood to supply the needs of transpiration is well established, but the mechanism of this rise has been much disputed. It is clear that any explanation must meet the extreme case of the tall leafy tree. Now a single tree may lose many gallons of water a day in transpiration and a blue gum tree (*Eucalyptus*) of Australia or a Sequoia of N. America may reach a height of 300 ft. or more. A mechanism has thus to be found which will not merely hold up a column of water at a height of 300 ft.—this is merely a problem in statics—but one that will drive (or pull) many gallons of water a day to this height. Many different forces have been invoked to explain the rise. The force of capillarity has been called in but measurements of the size of the wood vessels show that capillarity will not explain the rise of water to the height of a tall tree, let alone the continued movement of the water upward. Then again atmosphere pressure has been suggested as concerned in the movement, but such a pressure would only explain the rise of water to a height of a little over 30 ft. “Root pressure” has been called in as the motive power for the rise of the transpiration stream. When the stem of a wood plant is cut across near the ground a flow of sap under considerable pressure may occur from the wood of the cut stump; the pressure bringing about this flow is known as root pressure. Unfortunately for this explanation no pressures have been observed which are adequate to explain the rise of water to the top of a tall tree. Again root pressure is found most active in the spring, while the transpiration stream flows most actively in the summer. Then again we have the so-called *vital theories* of the cause of the ascent of sap in all trees. In these theories the living parenchyma cells which are so characteristic of the wood are supposed to exert a pumping action. They are assumed to take water from a lower wood vessel and pump it into a higher vessel with which they are in contact.

The objections to these vital theories are mainly twofold; they are inconsistent with experimental data and also with the known structure of the wood. The strongest experimental evidence against vital theories is obtained from the results of poisoning experiments. E. Strasburger carried out in 1893 some classical experiments with an oak tree over 70 ft. high and with tall climbers like wistaria and hop. The oak was cut off at the base and the cut end placed in a tub of picric acid, a highly poisonous yellow solution, which was found to be taken up in considerable quantities. After three days in this fluid the trunk was placed in a solution of a reddish dye (fuchsin) and there left for another six days. The oak trunk was then split down the middle when it was found that the yellow poison had been drawn up to 70 ft.,

and among the yellow stained wood were red patches showing that the dye had been drawn up *after* the picric acid, *i.e.*, through the *dead* wood. In the case of the two climbers lengths of 30–40 ft. were killed by heat when it was found that, as in the oak, coloured solutions were drawn up through the stems in spite of the killing of the living cells. These experiments seem to show clearly that fluids will rise in the wood of tall plants without the intervention of the living cells of the wood.

**Cohesion Theory of the Ascent of Sap.**—It is evident that in the absence of a pumping mechanism in the wood itself the water rising must *either be pushed from below or pulled from above*. Since water will rise even in tall trees when they are severed at the base some pulling force from above would appear to be acting and it can be demonstrated that a cut leafy shoot does exert a pulling or sucking force on a column of water. If a glass tube is fixed with an airtight junction to the lower end of a small leafy branch of a tree (the wood being bared at the point of junction), water will naturally rise in the tube. If the tube is filled with boiled water and the lower end placed in a dish of mercury, the mercury will be drawn up after the water. Under favourable conditions when no air bubbles develop in the system the mercury column will be raised *to a height above that of the barometric column*. This demonstrates that the cut branch exerts a definite sucking force on the water column. The same fact could be demonstrated without mercury using water alone in the tube, if the space above the water in which the tube dipped was exhausted of air. More elaborate experiments of this type show that a transpiring branch will exert a pull of 7 to 8 atmospheres. Such experiments demonstrate not only the sucking force exerted by a cut leafy shoot but also a peculiar physical property of a fluid such as water and mercury, namely, its cohesion or tensile strength. If a column of water or mercury is held up in a vertical tube without being supported from below, it must evidently be held by a pull from above. If, however, the fluid is transmitting a pull its particles must cohere together like the particles of a steel wire. Now it is found that if a fluid, like water, be free from air bubbles and is enclosed in a rigid tube to the wall of which the fluid *adheres*, it can then transmit a very considerable tension, owing to the attraction of the water particles for one another which is spoken of as their *cohesion*. Under conditions spoken of, with the fluid adhering to the walls of a rigid tube, the fluid is unable to change its shape and hence, as the result of its cohesion, is able to transmit a pull like a steel wire. By experiment it has been shown that in the case of water this cohesion or tensile strength is very great, for it requires over 200, and probably over 300, atmospheres to rupture a column of water.

The cohesion theory of the ascent of sap asserts that the water threads in the water channels of the wood are adhering to the wet walls of these vessels (and of the tracheids) and that these water threads can transmit any pull exerted on them at the top. Any cross-walls in the wood channel do not interfere with the practical continuity of the water columns since these walls are fully soaked with water. As has already been explained transpiration losses take place from the cells abutting on the intercellular spaces in the leaf, with a consequent increase in their suction pressure. As a result they take water from neighbouring cells and those with rising suction pressure will take water from the tracheids found in the fine vascular bundles (veins) of the leaf. The water columns in these dead tracheids are continuous with those in the rest of the wood channels in the plant, and the result of the withdrawal of water by the leaf cells is that these columns fall into a state of tension which is transmitted throughout the plant and thus down to the roots. The pull of the mesophyll cells in the leaf is thus felt by the cortical cells of the absorbing root, and water is drawn from them into the wood and their suction pressure goes up. This leads to water being taken from cells farther and farther towards the outside of the root, and so to loss of water from the root-hair which takes water from the soil; thus the chain of cohering particles extending from the soil to the leaf is complete.

**Difficulties in the Cohesion Theory.**—The cohesion theory cer-



tainly provides the most satisfactory explanation of the rise of the transpiration stream in tall trees. There are one or two difficulties, however, presented by the theory, one of which is in respect of air bubbles in the woody tracts. If sections of the wood are cut with great precaution a certain number of the wood channels are always found to contain air bubbles and therefore to be out of action. If the number of these air-containing channels went on increasing from year to year the proportion of blocked channels might be very high, though the new ring of wood laid down each year would start without air bubbles. It is suggested by Dixon that root pressure which develops in the spring would compress the air bubbles, by pushing the columns from below, and so cause their solution. It is doubtful, however, if root pressures occur of the magnitude necessary to bring about the solution of the bubbles at the top of a tall Sequoia tree. On the other hand the bubbles found in sections of the wood may be artefacts, *i.e.*, produced in the cutting of the sections. From the observations of H. R. Bode it seems doubtful if bubbles exist at all in the water-conducting tracks of herbaceous plants under normal conditions, and the case may be the same in woody plants, though the bubbles seem to develop very easily; this question of air bubbles in the wood requires further investigation. Another difficulty lies in the behaviour of dead leaves. The cohesive theory it must be remembered is a *purely physical* theory. All it requires is one membrane evaporating into dry air, another membrane in contact with a water supply, and the two connected by a continuous water thread under such conditions that it can support a tensile stress. Accordingly if we kill a leaf with chloroform vapour while still attached to the plant it should continue to draw up water as its cell walls are still directly continuous with the water supplies of the stem. One would expect the leaf cells to collapse owing to the loss of osmotic pressure but not to dry up; we find, however, that such a dead leaf soon dries. This suggests that though the cohesion theory rightly envisages the main factors in the rise of water there are other subsidiary factors which play a part.

#### ABSORPTION OF SALTS AND PERMEABILITY

As is well known the plant contains considerable quantities of inorganic salts of sodium, potassium, calcium, magnesium and iron and the only source of these is the soil from which nitrates, sulphates and phosphates are also obtained. The water in the soil is not pure but is a weak solution of inorganic salts known as the *soil solution*. The exact composition of the soil solution is doubtful. It must vary much from soil to soil and from time to time in the same soil and it is a matter of great difficulty to separate it from the soil. Estimations give a concentration of total solids in the soil solution from a wet soil of 0.1 to 0.025 per cent or less; a manured soil gives a stronger soil solution than an unmanured one. It is from the soil solution that the ordinary land plant takes up the salts necessary for its growth; unless the essential salts can be supplied in sufficient quantity growth will suffer. It must be added however that a sufficient supply of water and appropriate salts together with a sufficient aeration of the root system are not in themselves sufficient; in addition, the reaction of the soil must be suitable. The soil must be neither too acid nor too alkaline, or to put it more accurately, the concentration of hydrogen ions in the soil must be correct. Olsen (1923) in studying Swedish vegetation demonstrated a remarkable agreement between the concentration of hydrogen ions in the soil and the distribution of various plants. The presence of lime or chalk in the soil is of great importance in relation to soil reaction since lime neutralizes acidity. The addition of lime will often raise an infertile "sour" soil to a fertile level. The striking response of some plants to lime-rich or lime-poor soils may be related to the hydrogen ion concentration of the soil.

**The Essential Salts.**—Plants which normally grow in the soil can be grown successfully in water cultures, *i.e.*, in a solution of salts, or in quartz sand watered with such a solution. A solution of this kind may consist of water 1,000 grams, potassium nitrate 1 gm., calcium sulphate 0.5 gm., magnesium sulphate 0.5 gm., calcium phosphate and ferric phosphate each 0.25 gm. In this or

similar solutions plants may be grown successfully for many generations. If any of the elements, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium and iron are absent, the plant suffers, indicating that these elements are essential to the plant. The sodium and chlorine which plants absorb from the soil do not seem to be essential for plant growth. Moreover, small quantities of boron are absolutely necessary for the proper growth of such a plant as the broad bean. We know, in addition, most of the essential salts appear to be poisonous when given alone and that salts have an *antagonistic* action to one another, each neutralizing the toxicity of the other. The culture solution has thus to be a *balanced solution* in which the various toxicities cancel out.

**Absorption of Salts.**—When the water relations of the cell were discussed it was pointed out that the plasma membrane of the cell was of a semi-permeable nature, in that it held back soluble substances in the cell sap while showing a permeability to water. The fact that plants contain inorganic salts which they have taken up from the soil shows that the cell is not completely impermeable to dissolved substances, as does the fact that such substances as sugar travel about the plant. It is found, as we should expect that when salts (such as potassium nitrate or sodium chloride), or even cane sugar, are used as plasmolysing agents that the substance enters sooner or later and plasmolysis disappears. The entry of salts into the cell raises the whole question of the nature of the living plasma membrane and the forces which are concerned in bringing about the passage of substances in and out of the living cell. The subject, however, is as yet a very confused one and has recently been reviewed by Stiles. On simple physical principles a salt should go on entering and accumulating in a cell until the concentration inside and outside the cell is the same. If, however, a slice of carrot is placed in a solution of potassium chloride the salt goes on accumulating in the cell until the concentration inside is apparently many times (even 25 times) that outside. Again as Osterhout has shown, if the sap of the large cells of the seaweed *Valonia* is analysed it is found that the concentration of potassium inside the cell is over 40 times that of the sea water outside. On the other hand the concentration of sodium is five or six times as great in sea water as it is in the cell sap. The fact that the living plasma membrane can keep permanently between its two sides so great a difference of concentration as that of potassium shows that it must be of very peculiar nature.

**Changes of Permeability.**—As might be expected from the fact that the accumulation of substances in a cell is a fluctuating quantity one finds that the permeability of a cell is not constant; in other words the rate of entry or exit of a given substance may be changed by external conditions. For example the permeability of a cell to a particular dye may be markedly affected by the nature and concentration of a neutral salt in the dye solution. Since the plasma membrane contains a high percentage of protein and the physical condition of such substances is altered by many salts, the change in permeability is not unexpected. Then again we find that the rate of entry of one salt into a cell is altered by the presence of another salt. Weak solutions of sodium chloride and calcium chloride, which by themselves do not plasmolyse a cell, will do so when mixed. The effect seems to be due to the calcium ion altering the membrane in such a way as to hinder the entry of the sodium ion—another example of antagonistic action. Again it has been claimed that light increases the permeability of the cells in the leaf of the lime. Illumination has been definitely shown (Brooks, 1927) to increase the rate of entry of a dye into the *Valonia* cell, and also to increase the rate of diffusion of the salts from the cut surface of a tissue, such as that of the swelling at the base of the leaf-stalk in the sensitive plant (*Mimosa*). We have probably to view the permeability of active cells as constantly varying, though how the changes in permeabilities of neighbouring cells are related so as to cause material to travel in any particular direction in a tissue is still obscure.

**Transport of Salts and of Organic Substances.**—The mechanism of the transport upward of mineral salts and the transport downwards of organic substances (such as sugar from the leaves), is still imperfectly known. Owing to the apparent slowness of diffusion of salts from cell to cell the supplies of salts



required by the leaves would seem necessarily to move in the transpiration stream. There are, however, no data available showing that the rate of the stream and the concentration of salts in it are sufficient to transport the necessary supplies. A reduction of the rate of the transportation stream by shading leaves does not appear to reduce the salt content of the plant, at least in the herbaceous plants investigated. It may be that a certain critical rate of the stream is required and that in the experiments mentioned the rate was always above this.

### GENERAL METABOLISM OF THE PLANT

The term metabolism is applied to the whole complex of chemical changes going on in the plant, the building up of more complex organic substances from simpler ones being spoken of as *anabolism*, and the breaking down of complex to simpler ones being termed *katabolism*. It has already been noted that very many of the chemical reactions in the plant are balanced or reversible ones, so that according to the conditions (*e.g.*, the concentration of the reacting substances) the process may at one time be anabolic, another time katabolic. A balanced reaction ultimately reaches an equilibrium point where the rate of the process in one direction is equal to the rate in the other; the equilibrium is thus a dynamic one. In those balanced reactions in which there is an energy exchange, *i.e.*, heat is taken in or given out, the equilibrium point is altered by a change of temperature. Experiment in the laboratory shows that the rate of many chemical processes is markedly affected by a rise of temperature, the rate of many of them doubling for each rise of  $10^{\circ}$  C. The marked effect of temperature on the metabolism of plants is no doubt partly one of acceleration, and partly a shifting of the equilibrium points of reversible reactions. There is a further point in relation to balanced reactions; if such a reaction is proceeding in a particular direction and material A is being converted into material B, then the mere accumulation of B tends to slow down the reaction and ultimately brings it to a standstill; should then the amount of B be increased further the reaction will proceed in the other direction, *i.e.*, from B to A. A similar result is very common in reactions caused by enzymes, the accumulation of the products of the reaction tending to bring the reaction to a standstill.

Stress must be laid on the fact that the chemical processes going on in the living plant take place not in a simple homogeneous medium like water but in the protoplasm, which is what is called a *heterogeneous system*, having many colloid phases. (*See above.*) The enzymes which seem to play so large a part in metabolism also appear to be colloidal at least in part; thus many of the reactions may take place on their surfaces and on the surfaces of the protoplasmic medium. The system in which the chemical changes occur being thus heterogeneous and of so complex a nature, we should naturally expect that a variation of conditions (such as of temperature, illumination, etc.) would affect differently the processes in the plant and similar processes occurring in the laboratory.

The metabolism of the green plant, to which our brief review must be confined, shows two main anabolic processes, (*a*) the manufacture of carbohydrates in the process of *photosynthesis* (*carbon assimilation*), (*b*) the building up of complex nitrogenous substances such as proteins from nitrates absorbed from the soil and from organic material such as carbohydrates. In addition there is a main metabolic process, that of *respiration*, which is akin to the process of alcoholic fermentation by yeast.

### PHOTOSYNTHESIS (CARBON ASSIMILATION)

The whole life of the globe is dependent on this photosynthetic power of green plants for they alone are able to manufacture food material for themselves. The green plant may be described as the great alchemist which alone of living things has mastered the secret of converting the sun's rays into food material. The process of assimilation is associated with certain pigments which absorb the incident light; the energy so obtained is employed in the building up of complex organic substances from carbon dioxide and water, oxygen being at the same time evolved. In the case of the higher plants the pigments of the green leaf, as we know

mainly from the work of Willstätter and his collaborators, are four in number—*Chlorophyll a*,  $C_{55}H_{72}O_5N_4Mg$ , a blue-black crystalline substance, greenish blue in solution; *Chlorophyll b*,  $C_{55}H_{70}O_6N_4Mg$ , a green-black substance, green in solution; *Carotin*,  $C_{40}H_{56}$ , an orange-red substance found also in carrots, and *Xanthophyll*,  $C_{40}H_{56}O_2$ , a yellow substance. The two first are the green pigments and are often termed "chlorophyll," the other two are the yellow pigments. The amounts of these do not vary greatly in different leaves. The average amounts are given below:—

	Percent of fresh weight	Percent of dry weight
Chlorophyll a . . . . .	0.2	0.63
Chlorophyll b . . . . .	0.075	0.24
Carotin . . . . .	0.017	0.05
Xanthophyll . . . . .	0.033	0.09

In green algae the same four pigments are present; in the brown and red algae and blue-green algae chlorophyll is present in association with other pigments which give these plants their peculiar colour. The assimilating pigments are not dissolved generally in the cell but are associated with denser portions of the protoplasm of definite form, known as plastids; it is apparently in these plastids that the special physical and chemical processes characteristic of photosynthesis occur. It is generally accepted that the two green pigments are the most important in the process of photosynthesis. One of the functions of the green pigments is clearly that of absorbing the necessary energy for the decomposition of carbon dioxide, and their solutions show very characteristic absorption bands, particularly in the red-orange and the violet end of the spectrum. Whether in addition the chlorophyll reacts chemically with the carbon dioxide is still in doubt. Willstätter and Stoll hold that the carbon dioxide combines with the chlorophyll to form a definite compound on which light acts; it is thus converted into a substance of the nature of a peroxide which can be acted upon by an enzyme.

**Products of Photosynthesis.**—Sachs (1862) was the first to relate the carbohydrates appearing in the leaf to the process of assimilation; he was responsible for the dictum that starch was the "first visible product of assimilation." This was based on the fact that in the case of many plants starch appeared in the plastids of the leaf in the light and disappeared again in the dark. It is now generally agreed that carbohydrates of some kind are the main products of photosynthesis, though many monocotyledons form little or no starch, but much sugar in the form of glucose, fructose and cane sugar. Which carbohydrate is first formed is a matter in dispute. In green leaves exposed to light cane sugar accumulates markedly; this has led to the view that it is the first formed sugar. A much more plausible hypothesis would seem to be that hexose sugars (glucose and fructose) are first produced, and that when these reach a certain concentration cane sugar is formed from them; this view is supported by the work of Weevers (1924). The starch arises in all probability from glucose and it would seem likely that there is a critical concentration of sugar in the chloroplast above which starch is formed from the sugar, and below which the starch is converted back into sugar. This is confirmed by the fact that by floating leaves on sugar solutions of high concentration even those which are normally starch-free will produce that substance in their chloroplasts.

**Effect of Various Conditions on the Rate of Photosynthesis.**—The rate of this process is affected by the concentration of carbon dioxide available, by the amount of water, by the intensity of the light and by its wave length, by the chlorophyll content, by the supply of oxygen and of mineral salts, and also by many other internal conditions, or factors as they are called. It used to be supposed that all these factors acted independently, but it was shown by the work of F. F. Blackman (1905), that the factors are closely interrelated. He put forward the "theory of limiting factors," that in any set of conditions the rate of a physiological process was determined by the factor present at the lowest intensity. The view that under any set of conditions it was only by the increase of the intensity of one factor that the rate of the



process could be increased requires some modification in the light of recent work. It is clear, however, that if any factor A is present at very low intensity it will prevent an increase of another factor B having the marked effect upon the rate of the process which it would have produced if the factor A were acting at a higher intensity. Bearing this relationship of the factors in mind, we find that with increasing concentration of carbon dioxide the rate of assimilation goes up proportionally, if the concentration is not too high and light and temperature are sufficient. Similarly with increasing light-intensity the rate of assimilation goes up proportionally if the temperature and concentration of carbon dioxide are sufficient. With high light intensities there is probably a falling off in the rate, as with higher concentrations of carbon dioxide. With a moderate temperature, if other conditions are favourable, the rate of assimilation obeys the Van't Hoff rule, approximately doubling for each rise of temperature of  $10^{\circ}\text{C}$ . At higher temperatures, somewhere in the neighbourhood of  $25^{\circ}\text{C}$ , with some plants, the injurious effect of high temperature appears and the rate begins to fall off. The process of assimilation is little sensitive to the concentration of oxygen, reduction to  $\frac{1}{100}$  of the normal amount having no effect, but complete absence of oxygen acts injuriously. A number of *internal* factors must markedly affect the rate of photosynthesis, but the only one that has been closely investigated is that of the chlorophyll-content, by Willstätter and Stoll. It was found that the photosynthetic rate per unit of chlorophyll (the "assimilation number") varied markedly in different plants and even in the same plant. Leaves of yellow varieties were found to show very high rates in proportion to the amount of chlorophyll present, though the rate in these leaves is less influenced by temperature than is that of fully green leaves. Clearly there is some internal factor (or factors) other than chlorophyll content which is controlling the rate. This may be termed the "protoplasmic factor"; Willstätter and Stoll conclude that this factor is enzymic.

**Quality of Light and Photosynthesis.**—The question of the effectiveness in photosynthesis of light of different wave lengths has been hotly debated by physiologists for many years. The question is a complicated one since in white light there are great differences in the energy-value of the rays of different wave lengths, and the different rays are absorbed to a very different degree by the chlorophyll and the colourless parts of the leaf. In the case of the leaf there is little doubt that with equal intensity of incident light the red rays are more effective than the blue. The work of Warburg and Negelein quoted below indicates also that for equal quantities of light-energy *absorbed by the chloroplast*, the red rays are considerably more effective than the blue.

**Efficiency of the Photosynthetic Process.**—It is known that the green leaf is comparatively inefficient as a producer of assimilation material. Brown and Escombe (1905) attempted to determine the efficiency of the green leaf by comparing the energy of the light absorbed with the absorption of carbon dioxide, the assumption being made that glucose was produced in the leaf from the carbon dioxide. Their results are only very approximate but they indicate that the efficiency is only about 1%, increasing however with low intensities of light to about 4%. A large proportion of the energy absorbed is used in transpiration, and with the higher intensities of light the concentration of carbon dioxide in nature is too low to allow of the light being fully effective. The most accurate experiments on the efficiency of the photosynthetic process are those of Warburg and Negelein (1922 and 1923) with the minute unicellular fresh water alga, *Chlorella*. With such a plant there is no question of transpiration, and the experimental arrangements were such that practically the whole of the light received was absorbed by the chloroplasts of the cells; in the case of the leaf a considerable amount of the light passes through it and a certain amount is reflected. Warburg and Negelein show that with decrease in the intensity of the light the efficiency goes up, *i.e.*, a larger proportion of the light absorbed is made use of in photosynthesis, the rate of the latter process being measured by the production of oxygen. In their earlier experiments they obtained an efficiency of 71% when using yellow and yellow-red rays; the methods employed for calculating this were, however, not

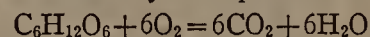
altogether satisfactory. In their later work they obtained results of 59% for red light, and 34% for blue light. Whether these percentages are the maxima that can be obtained is not yet certain.

**Cosmic Relations of the Photosynthetic Process.**—As already stated this process is the fundamental chemical process on which the life of all animals and plants depend. A study of the land plant's relation to the sun shows it as a machine of comparatively low efficiency, since only a small part of the sun's energy is stored by the plant, crops such as cereals and potatoes retaining only 2 to 3% of the energy received. This uneconomical working is in part due to the fact that so much of the sun's energy consists of invisible heating rays which the plant cannot use for food production. Furthermore the plant is somewhat more efficient than first appears as part of the material manufactured during the day is burnt up again in respiration and so lost. The proportion so lost is very variable, depending largely on the temperature at night; it may be taken as 20–50 per cent. Another cause of the low efficiency of the plant, as has already been pointed out, is the low concentration of the raw material (the carbon dioxide) available for the process. It has been suggested that in early Carboniferous times when coal was formed, the concentration of this gas was higher. However this may be it is clear that the energy available from our rapidly lessening stores of coal and oil is really the energy of sunlight received by the earth many thousands of years ago.

## RESPIRATION AND FERMENTATION

Respiration and fermentation are closely allied processes. Both consist in the breaking down, generally by an oxidation, of complex organic compounds, commonly sugar, into simpler ones with a liberation of energy. In respiration oxygen is usually necessary and the breakdown is complete, carbon dioxide and water being formed. In the second oxygen is not necessary and the chemical degradation is not complete, some organic substance such as alcohol being the end product. As is to be expected the release of energy for a given amount of sugar consumed is much greater in respiration than in fermentation, the first being a much more economical process than the other. By means of these two processes the plant gains supplies of available energy from the food material consumed. Such supplies of energy are necessary to maintain the dynamic equilibrium of the cell and to carry on various chemical processes in which energy is absorbed. In the higher plants some of the energy is also used in mechanical work.

**Aerobic Respiration.**—As has already been stated absorption of oxygen and the production of carbon dioxide are characteristic of the majority of plants as they are of animals. The carbon dioxide is not the only product for if sugar is oxidized an equal number of molecules of carbon dioxide are formed together with a certain amount of heat. The term *aerobic* respiration is applied to this process in contrast with the one in which oxygen is not necessary, which is termed *anaerobic* respiration and is akin to fermentation. Various substances appear capable of being oxidized in respiration, sugars, fats, proteins, sulphur, ammonia, nitrites, methane, ( $\text{CH}_4$ ) hydrogen, etc., but in the higher plants sugar seems to be the substance most commonly consumed. The action is an oxidation and may be expressed thus:—



together with a release of 674,000 calories of energy.

The intensity of respiration varies enormously in different plants and different organs of the same plant. Actively growing tissues such as meristematic tissues show the most intense respiration, in some cases as in the developing spadix of arum (*see* ARACEAE) the rate is as high as in warm blooded animals and the heat generated is sufficient to raise perceptibly the temperature of the inflorescence. Developing seeds also show active respiration; poppy seeds at  $16^{\circ}\text{C}$  give out in 24 hr. 122 cc. per gram of *dry* weight. Leaves pressed together in a receptacle where heat losses are small may in the process of respiration raise the temperature so much as to bring about their death. When sugar is used in respiration the amount of carbon dioxide given out is equal to the amount of oxygen taken in; the *respiratory quotient* ( $\text{CO}_2/\text{O}_2$ ) is then one. In other cases it is widely divergent from unity espe-



cially when fats or proteins are being consumed.

**Effect of Conditions on Respiration.**—The rate of this process is markedly affected by various external and internal conditions. Temperature is one of the most active as is to be expected, since a rise of temperature tends to accelerate chemical processes generally. The effect on respiration is very similar to that on assimilation (*see above*) and again markedly depends on the duration of exposure to higher temperatures. The respiration rate is very low round about the freezing point, but rises with increase of temperature, being very approximately doubled for a rise of temperature of  $10^{\circ}\text{C}$ . After a time, however, an injurious effect with rise of temperature sets in—no doubt an effect on the protoplasmic mechanism, since high temperatures affect colloids.

The rate of respiration is also affected by the amount of the available material. Increase in the concentration of sugar supplied tends to raise the rate, as can be shown by adding or subtracting sugar from the food supply of a fungus in culture. A reduction of the amount of oxygen in the air has not much effect on respiration until the amount is considerably reduced. On the other hand the accumulation of carbon dioxide—a product of respiration—has a definitely depressant effect on the rate of both aerobic and anaerobic respiration.

**Anaerobic Respiration and Fermentation.**—Green plants which normally show aerobic respiration are still able to give out carbon dioxide when kept in an atmosphere free from oxygen; at the same time alcohol is produced in small quantities indirectly showing kinship between fermentation and this type of respiration. The alcoholic respiration of yeast has been the subject of much investigation and is known to be associated with an enzyme—*zymase*, and the production of a compound of sugar and phosphoric acid (known as hexosephosphate) and an enzyme which acts on this compound. (*See FERMENTATION.*) The work of Neuberg and his collaborators indicates that pyruvic acid is an intermediate product between sugar and alcohol.

**Mechanism of Respiration.**—The peculiarity of respiration as a chemical process lies in the fact that the plant (and animal) is able to oxidize at quite ordinary temperatures such a substance as sugar, which in the laboratory can only be burnt at high temperatures. The question arises as to the peculiar conditions in the plant responsible for this. Oxidizing enzymes have been claimed as the key to the problem, but while these will readily oxidize certain aromatic compounds they will not act on the respiratory substances such as sugars. Wieland has brought forward an entirely different theory of physiological oxidation in which water is the real source of the oxygen used. In this view the first step in the process is the combination of the respiratory material with water, which is followed by a process of *dehydrogenation*, probably under the action of an enzyme, in which hydrogen is split off leaving the material oxidized. The hydrogen is in an active state and in ordinary aerobic respiration combines with the oxygen of the air to form water; the oxygen of the air thus acts as a *hydrogen acceptor* as it is called. In the absence of air other substances, such as methylene blue or hydroquinone, can take its place. Thus the oxidation of acetic acid to alcohol can go on without oxygen if methylene blue is present. Glucose also can give carbon dioxide at ordinary temperatures when water and some catalyst, such as palladium black, are present and some acceptor of hydrogen is available. Another theory is that of O. Warburg, who holds that respiration is essentially a surface reaction. He has shown that various substances such as oxalic acid, amino acids, and even sugars are respired in the living organism. The effect of narcotics on the “respiration” of the surface is very similar to that on the respiration of the living organism. Quastel’s theory of the activation of the respiratory substances and the discovery by F. G. Hopkins of the important sulphur-containing substance glutathione must be referred to. The various theories of oxidation are discussed in the English edition of Kostychev’s book on plant respiration (*see references*).

## GROWTH

The term growth is generally applied to the increase in size of an organism. In unicellular organisms it applies only to the

increase of the single cell; in multicellular organisms it is generally associated with the formation of new cells as well as with the increase in size of cells already existing. In the growth of the cell we may find an increase in all the cell constituents, cell-wall, protoplasm, etc., though frequently an increase in volume is brought about by the enlargement of the volume of the cell without any increase of protoplasm. Of the manner of growth of protoplasm we know very little. Bacteria (which are unicellular and consist of little else than a mass of protoplasm) when placed under the more favourable conditions of temperature and food supply will multiply so rapidly that each cell divides into two new ones every 20 minutes. The protoplasm thus grows at such a rate that its mass becomes multiplied *eight times every hour*. This shows that the production of protoplasm from non-living material may go on at an astonishing rate, but of the details of this production we are quite ignorant. In cells invested with a cell wall the growth of the latter is due to the activity of the protoplasm. The new wall which divides the parent-cell into two new ones is formed across the nuclear spindle. (*See above, Cytology.*) There has been considerable dispute as to the method of thickening of a wall already formed, whether it is by the addition of new layers, *i.e.*, apposition, or by the intercalation of new particles of cell wall material among the old—the so-called *intussusception*. It is probable that the first process is the more common but that both occur.

**Effect of External Conditions on Growth.**—It is found that on the whole light has a retarding effect on growth. When illuminated the actual length attained by the organ and the rate of growth are both less than in the dark. Dicotyledonous plants grown in the dark have generally much elongated stems and also small leaves but the actual amount of light required to prevent the *etiolated* condition is very small. Light is of course indirectly necessary for the growth of the green plant, as without it the leaves are unable to build up the food material. *Temperature* is the factor which has the most marked effect on the rate of growth, as is to be expected since the temperature so largely controls the rate of the processes on which growth depends. There is a *minimum* temperature below which the growth of the plant or organ does not occur at all, a *maximum* above which the growth stops as a result of injury to the plant, and an *optimum* temperature, the one at which the rate is greatest. These, however, are not absolute terms for, as with all effects of temperature, the degree of temperature cannot be separated from its duration. This is so particularly in relation to higher temperatures which may be injurious only when the duration is prolonged. In the case of the roots of the cress plant, which have been closely investigated, the minimum is found about freezing point,  $0^{\circ}\text{C}$ ; the optimum, however, was found to vary with the duration of the exposure. If the roots were tested by means of an exposure of  $3\frac{1}{2}$  hours to various temperatures, the optimum was at  $30^{\circ}\text{C}$ ; with an exposure of 7 hr. at  $29^{\circ}\text{C}$ , while with an exposure of 14 hr. the optimum was pushed back to  $27^{\circ}\text{C}$ . The maximum also was found to fluctuate in a similar manner being higher with shorter times of exposure. Both light and temperature have also a *formative* effect on the plant in that these factors may affect the shape of plant organs; plants grown at high temperatures in weak lights are noticeably different in appearance from plants grown at a lower temperature and a higher light intensity. The formative effects of chemical substances is also often marked at least in the case of the lower plants. Another external condition necessary for the growth of most plants is a supply of oxygen.

**Periodicity of Growth.**—Organs of limited growth usually show what is called a “grand period of growth,” the rate of growth being at first slow then gradually increasing to a maximum and then slowing down again to zero. This may be illustrated by a zone on the main root of a bean seedling which in *successive days* showed the following increases, the results being expressed in millimetres, 1.8, 3.7, 17.5, 16.5, 15.5, 14.5, 7.0, 0.0. If we express the total length of the root section graphically we have an S shaped curve; the organ or plant body starts as a small structure, grows at first slowly and then with increasing rapidity, and then the rate of growth begins to slow down and finally stops.



**Correlation of Growth.**—One of the most striking phenomena in the growth of the plant body is the correlation of growth. The thickness of the trunk is related to the size of the branches which it bears, and the size of the root-system is correlated with that of the shoot-system. A good example of correlation is seen in the bending up in a side-shoot to replace the loss of the top of the main stem in the tree trunk of a conifer. It has been known for some time that in the animal body hormones (chemical messengers) are produced by certain glands and that these hormones circulating about the body may control growth and other processes. It has of recent years been demonstrated that the plant possesses growth-promoting substances which can diffuse through the plant and so control growth at some distance from the point of production of the substances.

### IRRITABILITY

The term irritability is often applied to the visible reactions which the plant makes to its environment. The particular action of the environment is known as the *stimulus*, and irritable responses as responses to a stimulus. The stimulus may, for example, be some change in the intensity of light or temperature or gravity or electricity. Some stimuli are necessary for the normal growth of the plant such as a suitable degree of temperature, light, etc.; without such conditions acting more or less continually on the plant body as a whole the organism would not be in a state to react to stimuli. The term stimulus is to a large extent a term serving as a cloak for our ignorance. We do not speak of the stimulus of light causing assimilation because we have some physio-chemical picture of this process. When a shoot turns in response to unilateral light we speak of the light as a stimulus, largely because we are unable to picture the course of events which cause difference of illumination to bring about curvations of the shoot or root. Stimuli have, however, usually one point in common that the stimulus does not itself supply the energy employed in the response to the stimulus, but the energy used in the response comes from a store pre-existing in the plant. The stimulus seems thus to be a releasing mechanism, in which the amount of energy employed has no relation to the energy released. The firing of a gun is a good example where the energy used in pulling the trigger has no relation at all to the amount of energy released in the explosion; irritable mechanisms of this kind are therefore sometimes called *trigger mechanisms*.

### GEOTROPISM

It is well known that the plant body takes up a definite position in space. The main stem of a tree usually stands quite vertically and its branches stand out more or less horizontally. The main or tap root also grows vertically downwards and the root-lets at various angles. It is well known also that if a seedling is placed with its stem and its root horizontal the stem proceeds to curve upwards and the root downwards.

**Geotropic Response.**—This response is known as a geotropic response, that of the stem being *negatively geotropic* and the root *positively geotropic*. We note that the curvature is usually confined to the tips of the organs, *i.e.*, to the growing points of the stem and the root. That the curvature is due to the action of gravity was shown as long ago as 1806 by Knight, the English experimenter. He fixed a number of seedlings in different positions on the edge of a wheel rotating in a vertical plane, that is, on a horizontal axis. The wheel was rotated at a considerable speed so that at its edge there was considerable centrifugal force. The result he observed was that the roots, in whatever direction they had started growing, soon grew outwards at right angles to the direction of the axis. The stems, however, grew in the opposite direction to that in which the centrifugal force was acting and they soon all met in the centre of the wheel. This experiment shows that plants do not distinguish between gravity and centrifugal force, and that the root grows in the direction of the force while the stem grows in the opposite direction. About 70 years later Sachs invented his *klinostat*, an apparatus by which plants are rotated on a disc in a vertical plane, but the speed of rotation is very slow, once in 10–20 minutes. As a result centrifugal force

is negligible but the one-sided action of gravity is abolished as every side of the organ in turn faces downwards; the effect of gravity is not annulled but the curving (*tropistic*) effect is abolished. It is evident that the curvature results from the difference in the elongation of the two sides.

**Geotropic Curvature** is not confined to plant organs which are still in active growth. It may occur in organs which have normally ceased to grow as in the case of the stems of grasses. If a short piece of wheat or barley stem is placed in a horizontal position, the base of the node, to the growth of which the elongation of the node is mainly due, will start into growth again as a result of the stimulus of gravity and the stem turns upward. That such curvature is not a simple weight effect on the plant is shown by the *upward* curvature of the stem, and by the fact that the root often will grow downwards into mercury although in such a dense fluid the root tends to be forced upwards.

**Reaction and Presentation Time.**—As we are dealing with a stimulus we should expect the effect to be related to the duration, intensity and direction of the force; this we find to be the case. When a stem or root is laid horizontal the time taken for the organ to show a *visible* curvature is 10 to 20 minutes, according to the sensitiveness of the object and the external conditions, such as the temperature. This period is known as the *reaction time*. It is found that this length of time is not necessary to produce a curvature. If after a much shorter time the plant is removed from the horizontal position and placed on a klinostat, the curvature follows later. The minimum time to which the plant must be exposed to the gravitational stimulus in order to show later a curvature is known as the *presentation time*. This is much shorter than the reaction time and varies from as short a period as 2 min. for the inflorescence stalk of the plantain and the hypocotyl of the sunflower, to 25 minutes for some other plants. There is naturally a marked difference in the presentation times exhibited by individuals of the same species. In the oat shoot, for example, the mean time was 32 minutes, but some reacted in less than 14 minutes, while others required more than 49 minutes. It is found that the stimulation applied during the presentation time need not be given all at once. A series of short exposures, each less than the presentation time, may by *summation* become effective. If the pauses between stimulation are only five times as large as the periods of stimulation the presentation time is not lengthened by the intermittent nature of the treatment. Thus, if the normal presentation time of a shoot is 10 minutes, it will react if placed horizontal for five successive 2 minute periods, with a period of 10 minutes in the vertical position in between. If, however, the period between one stimulation and the next is 20 minutes, then more than 5 of the two-minute periods will be required. The effect of the stimulation thus slowly weakens during the pauses.

The presentation time and reaction time are naturally affected by the intensity of the applied stimulus. We cannot alter the effect of gravity, but we can use instead a centrifugal force which can be increased at will and to which, as has been shown above, plants respond as to gravity. The table below gives the intensity of the centrifugal force measured in terms of gravity (G), the presentation time, and the products of the time by the intensity.

Intensity	Presentation time	Product
46 G	7 secs.	322
24 "	12 "	287
4.84 "	60 "	290
0.76 "	415 "	315
0.14 "	2.230 "	322
0.04 "	7.800 "	312

We see from the third column that the geotropic reaction obeys what is called the *product law*—the time of stimulation is inversely proportional to the intensity of the stimulus, so that the product of the two is constant. This product law is also clearly shown when the root or stem is placed at various angles with the horizontal. The horizontal position is found to give the most intense stimulus, the intensity being proportional to the *sine* of



the angle with the vertical at which the organ is placed.

### PHOTOTROPISM

The fact that plants growing near a window will bend their shoots towards the light is familiar to everyone. This reaction is known as *phototropism*, which means a turning towards light; the term has replaced *heliotropism*, which means a turning towards the sun, since the reaction is shown in relation to almost any light. As in the case of geotropism there are two types of response, *positive* and *negative*, where the turning is towards or away from the source of light respectively. The first is found strongly marked in most shoots of the higher plants and is also found in a few roots. The positive phototropism of most roots is to be expected, since without some such response the light needs of the plant could hardly be satisfied. It is also to be noted that with the ordinary diffuse light of the sun the phototropic reaction is much more powerful than the geotropic. A seedling developing from a seed underneath a stone in a position to which light reaches, will not, under the influence of gravity, push its shoot fruitlessly against the stone above, but will show a phototropic curvature and so reach the light. Negative phototropism is found in some underground roots but markedly in the aerial roots found in many orchids. There are also plant organs which tend to set themselves at right angles to the direction of the incident light; these show *transverse* phototropism. The phototropic reaction is usually a growth reaction like the geotropic one. The side which becomes convex grows faster than the normal, and the concave side less fast. Also, as in the case of geotropism, unilateral light may cause a curvature in a mature organ by starting growth in length afresh. All light curvatures are, however, not due to growth changes but in the case of some leaves to the turgor changes of special cells.

**Phototropism and the Product Law.**—As with geotropism we find that the product law holds; the effect depends on the amount of light received, *i.e.*, on the product of the intensity of light multiplied by the time of illumination. The time required with different intensities of light to start a reaction, *i.e.*, the *presentation time*, is given below for the coleoptile (the seedling sheathing leaf) of the oat:—

Presentation time	Intensity (metre-candles)	Product
6 (hours)	0.00085	18.6
1	0.00477	17.2
4 min.	0.0898	21.6
4 (seconds)	5.46	21.8
$\frac{1}{100}$ (second)	1,902	19.0

It is seen that the product varies about the number 20, which means that the oat coleoptile will respond to 20 metre-candle-seconds. The principle of summation is also found with phototropism; stimuli too weak to cause a reaction will act if repeated. The intensity of the light required to produce an effect for a given time is found to vary with the colour, in other words, with the wave-length. It is found that *visible* light of all wave lengths will act, but the violet light is the most effective.

**Conduction of Stimulus.**—Charles Darwin showed as long ago as 1881 that the light stimulus might be perceived at one place and the curvature result at quite another place, showing that the stimulus was conducted. This is well seen in certain grass seedlings (such as those of *Setaria*), where the apical cotyledon soon stops growing, while the hypocotyl below continues to elongate for some time. Illumination of one side of the *cotyledon alone* will bring about a marked curvature of the hypocotyl below. In the same way unilateral illumination of the *tip* of the coleoptile of the cereal seedling, such as oat, will cause a curvation of the *lower* part. In relation to the conduction of the phototropic stimulus in this plant a very surprising result was obtained by Boysen-Jensen in 1913. He found that if the tip of the coleoptile be cut off and stuck in again with a thin layer of gelatine and the tip be then exposed to one-sided light a curvature will ensue in the darkened lower region. Later this was shown to be true for other grasses and also for the conduction of a stimulus due to injury. Snow in

1923 was able to show that the same held for the geotropic response of bean roots. If the tip is cut off and is fixed on again with gelatine the roots curve when placed horizontal. This suggests something which can pass a layer of gelatine, *i.e.*, very definitely a soluble growth-promoting substance which differs from the illuminated tip and causes the curvature. It has also been found that the slowing of the growth of a vertical coleoptile caused by decapitation can be largely removed by replacing the coleoptile in position. Such observations as these have led to a large amount of work, particularly in Holland and Germany. The most striking of the results obtained has been that of F. Went (1927), who has shown that by placing cut off illuminated coleoptile tips on small blocks of agar (a gelatine-like material obtained from seaweed) the growth-promoting substance diffuses into the agar. Blocks of this agar when placed on the cut surface of the coleoptile are able to cause curvatures.

**Nature of Phototropic Reaction.**—The earlier view of the positive response of stems to unilateral light was that the side towards the light being more highly illuminated had its growth rate reduced more than did the other side, with the result that the stem bent towards the source of light. Later, however, when the negative response of other plant organs was observed, and the response of transparent structures like root hairs and fungal hyphae, the view was widely held that the plant responded to the *direction* of the incident light. A. H. Blaauw was the first to return to the simpler theory; he showed that simple unicellular structures like the sporangiotheca of *Phycomyces* and the complex hypocotyl of the sunflower exhibited a complicated but definite "light-growth reaction" when equally illuminated all round, the rate of growth being increased in *Phycomyces* and reduced in the sunflower. Light *apart from direction* has thus an accelerating effect in the one case and a retarding effect in the other. The turning of the hypocotyl of the sunflower towards the light is easily explicable as the side towards the light would be more illuminated and so grow more slowly. In *Phycomyces*, however, a negative phototropism might be expected, since the "light-growth reaction" is one of retardation, but in fact the curvature is towards the light. Blaauw, however, pointed out that the glass-like cylindrical structure of the sporangiotheca acts like a lens and focuses the light on the further side, which is thus more intensely illuminated than the nearer. As a result of his work Blaauw put forward the view that in general the phototropic reaction is simply a growth response to differences of light intensity on the two sides of the organ.

The chemotactic movements of antherozoids and bacteria and the chemotropic movements of roots cannot here be dealt with, but a few words must be said on the so-called *nastic* movements of plant organs. These are movements which may be called out by a change in external conditions, but, as already stated, the nature of the movement is not determined by the stimulus from outside. The perianth leaves of the tulip exhibit a *thermonastic* movement, for when the temperature is raised these leaves open as a result of the greater growth of the upper sides. Many flowers show *nyctinastic* movements, opening and closing in response to changes of light intensity. Similar movements, the so-called *sleep movements*, are also known in leaves, especially in the leaves of Leguminosae.

**Photoperiodism.**—A very interesting reaction to light, which is in no sense a phototropic response, has been discovered of late years. It is a familiar fact that at least in temperate climates many plants flower only at certain periods of the year; there are so-called spring flowers, autumn flowers and plants which flower in the summer. This marked seasonal effect must be due to some varying external condition or set of conditions. It has often been supposed that temperature plays a large part in the development of flowers, and a certain degree of warmth is essential for growth, yet altering the temperature alone will not markedly alter a plant's flowering period. Asters and chrysanthemums cannot be made to flower in summer by lowering the temperature, nor irises in winter by putting them in a greenhouse.

Apart from temperature there is one regular cyclical change associated with the march of the seasons and that is the change in



length of the day and night, the day in the latitude of London varying from 16½ hours in June to a little under eight hours in December. It was shown by Garner and Allard that in the case of many plants it is the length of the day which is the decisive factor in fixing the season of flowering. The discovery was made in the United States, where the behaviour of a valuable variety of tobacco, known as Maryland Mammoth, was being studied. It had been found impossible to obtain seeds from this variety since it went on growing steadily through the season, sometimes reaching a height of 12 ft., being eventually cut down by frost before it had formed flowers. One autumn a specimen was transplanted to a greenhouse, where it promptly flowered and set seed. This was at first thought to be an effect of temperature, but further investigation showed that it was impossible to cause the plants to flower in summer. It was soon found that the *dominating factor was length of day*; if growth conditions were favourable it would flower in the short days of late autumn or winter but not in the long days of summer. By artificially shortening the day to 12 hours, by placing the Maryland Mammoth plants in the dark during some of the daylight hours, flowering could be brought about at any time of the year. Following up this discovery Garner and Allard investigated at Washington the behaviour of a large number of plants. These were grown in pots which were borne upon light trucks running on lines so that the pots could be run in and out of sheds and thus be illuminated for various fractions of the daylight period. Many plants, such as the tobacco variety mentioned above, soya beans, asters, chrysanthemums, poinsettia, were found to be "short day" plants, and would only flower when the period of daylight was reduced to 12 hours or less. If the time of illumination is suitably adjusted the plants will flower and fruit when they are quite diminutive, while other individuals exposed to full daylight grow to a large size without any trace of flower production. Other plants such as grasses have been shown to be "long day" plants, which require a long daily period of illumination for the initiation of flowering.

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## PATHOLOGY OF PLANTS

Plant pathology (or Phytopathology) is that branch of biological science which treats of the diseases of plants. While there can be no doubt that diseases of plants, and in particular of cultivated plants, have manifested themselves from time immemorial, it is only within comparatively recent years that their study has been taken up in an organized and scientific manner. The application of the scientific method generally to the study of practical agricultural problems is a development scarcely older than the 19th century.

**Historical.**—In view of the devastating effects of plant disease, especially when the particular plant attacked is of primary importance as food for mankind or his domestic animals, it is not surprising to find that references to epidemics of disease are not uncommon in historical writings, even of remote times. The earliest records are to be found in the Old Testament (*e.g.*, Deut. xxviii., 22, 1 Kings viii., 37) under such terms as "blasting" and "mildew." The precise nature of the diseases referred to cannot now be determined but there is little doubt that some of the epidemic diseases of cereals, such as rust or mildew, are indicated. The ravages of insects are frequently noted, such as for instance plagues of locusts, caterpillars and canker-worms.

In Greek literature we find references to plant diseases in the writings of Aristotle, and more particularly in those of his pupil Theophrastus, the father of botany. The latter describes diseases of a number of cultivated crops, such as various legumes, cereals, fig, olive, etc., and observes that varieties of the same crop may show different degrees of resistance to disease. This is probably the first mention of the idea of "resistant varieties" which figures so largely in present day writings on the subject. Among Roman writers the younger Pliny, who flourished in the 1st century of our era, devotes some attention to the subject and makes a number of well-founded observations regarding the incidence of certain plant diseases.

The middle ages were for plant pathology, as for all other sciences, dark ages and we have to come down to the Renaissance, with its general quickening of interest in all intellectual pursuits, to find evidence of further progress. The 17th and 18th centuries witnessed considerable activity in the study of plant diseases. The new studies proceeded in the main from two different directions. The practical gardener or agriculturalist was chiefly concerned in describing the various diseases to which his crops were subject and in attempting to evolve methods of treatment. On the other hand, the student of human pathology was interested in the diseases of plants from the possible analogies to his own problems which such a study might offer. The whole science of botany had in the old days a distinct medical bias. It is not surprising, therefore, that the study of plant diseases has been to a large extent modelled upon the older science of human pathology, the terminology of which has been freely borrowed.

The elucidation of the real nature of plant disease, from the point of view of the causal agent, is mainly dependent upon the perfection of the microscope. But even the extended powers of observation which the use of that instrument brought to bear on the subject did not at once lead to a correct appreciation of the true nature of plant disease. Various structures were observed and accurately figured in detail as being associated with the diseased parts, but they were interpreted as portions of the plant which had become changed by the disease and not as belonging to a distinct organism which was responsible for the disease. The first incontestible proof that a specific plant disease was due to the invasion of the tissues of the plant by a definite parasitic organism was furnished by the German scientist, De Bary, whose pioneer researches prepared the way for a host of other workers, at first chiefly in Germany, and later in all civilized countries. The 20th century has witnessed an extraordinary activity in the study of problems of plant disease, most strikingly, perhaps, in the U.S.A. The economic importance of the subject, as a branch of scientific agriculture, has become increasingly recognized and the prosecution of plant disease researches is being more and more taken up by Government departments in all countries possessing a progressive agriculture.





FROM (A, B, C, D) DUGGAR, "FUNGUS DISEASES OF PLANTS" (GINN & CO.), (E) SALMON & WARE IN JOURNAL OF MINISTRY OF AGRICULTURE (H.M. STATIONERY OFFICE), (F) WILTSHIRE IN "STUDIES ON THE APPLE CANCER"

FIG. 1.—TYPES OF PLANT DISEASES

A. Abnormal development of buds on branch of cherry giving rise to "witches' broom." B. Ergot of rye, showing replacement of grain by a fungal structure (Sclerotium). C. Finger-and-toe or club root disease of cabbage. D. Canker of apple tree. E. Spike disease of hop (Central branch diseased, lateral climbing branches healthy). F. Spotting of fruit disease "Anthracnose" of bean

**Definition and Scope.**—While it is true that the distinction between a healthy and a diseased plant is often perfectly obvious, it is not easy to frame a definition of the diseased condition which will meet all cases. The border line between health and disease is not always sharply marked. It will be shown below that the majority of plant diseases result from the invasion of the plant tissues by a definite organism, the *parasite*. Nevertheless, the presence of a parasite does not always necessarily mean disease in the common acceptance of the term. For example, the root-nodules of leguminous plants (pea, bean, clover, etc.) are produced by the attack of an organism—a bacterium—and far from producing damage, the presence of the bacterium is essential to the proper development of the plant. The important part played by certain fungi in the germination and subsequent growth of many plants, such as orchids and heaths, is a further illustration. The living together of two organisms does not necessarily produce injury to either partner, in which case one speaks of a *symbiotic* relationship. Every gradation may be traced from the purely symbiotic type, in which the two partners are benefited or not obviously injured, to the distinctly parasitic type in which one partner thrives at the expense and to the detriment of the other. In fact both types of relationship may be shown between the same two partners—that is, a symbiotic or harmonious relationship is at first set up, but by and by one of the partners suppresses the other and the relationship becomes one of parasitism. There is thus a gradual transition from a condition of health to one of disease.

So far reference has only been made to the diseases of parasitic nature. Over and above these there is a class of diseases in which no parasite is present at all, viz., the so-called *physiological diseases*. The existence of the latter increases the difficulty of defining disease in terms of the causal agent.

Perhaps the most adequate definition is obtainable by considering the normal development of a plant. Over a certain range of conditions, which one reckons as normal, a particular species of plant develops in a certain way—e.g., has a certain appearance, reaches a certain size, and so on—all of which are the reflection of

a normal physiology or functioning of the plant. If now a particular individual diverges from the normal and if the abnormality impairs the functioning and more especially imperils the life of the plant, that plant may be considered as being diseased.

From the purely practical or economic point of view, a satisfactory definition of disease presents no great difficulties. Any given crop is grown in the expectation of a certain yield, both as regards quality and quantity. Disease in its economic aspects may therefore be defined as a condition of the crop in consequence of which it fails to give a satisfactory yield.

**General Classification.**—Diseases, whether of plants or animals, may be classified on the basis of the symptoms produced or of the causal agent concerned. For reasons given more fully below, the latter system of classification is more generally adopted in connection with plant diseases, and it is convenient to give at this point a general classification along such lines in order to limit the scope of the present article. Classified on the basis of the causal agency, plant diseases are as follows:—

- (1) Diseases due to the non-living environment.
- (2) Diseases due to so-called *internal* causes.
- (3) Diseases due to living agencies, which may be plants or animals.

The first two groups constitute the *physiological* diseases. In group (1) the disease symptoms can be related to certain physical or chemical features of the environment. In group (2) no such association has yet been demonstrated, nor has it been possible to explain the symptoms as being due to the presence of a parasite. The second group is thus defined on purely negative characters, and is in fact a kind of limbo into which are put all diseases the cause of which is still obscure. Some of these may prove, with advancing knowledge, to be referable to either of the other groups.

The members of the third group constitute the *parasitic* diseases. The plant, technically termed the *host*, is attacked by another organism called the *parasite*. The animal parasite may be various—mammal, bird, snail, insect, eelworm, etc. The attack of a crop by such an animal as a rabbit is not usually described as a



disease, though there is no difference in kind between such attack and that produced by mites or greenflies. Economically the most important diseases of animal origin are those produced by insects, and these constitute in the main the province of the entomologist. (See ENTOMOLOGY: *Economic*.)

Plant parasites may be bacteria, algae, fungi (including slime-fungi) or higher plants. Plant diseases of bacterial origin were at one time believed not to exist, on account of the supposed fact that the acidity of plant juices is inimical to bacterial growth. Many bacterial diseases of plants are now known, some of great economic importance. The recorded cases of parasitism due to algae are few and unimportant. Diseases caused by higher plants, some of which will be cited later, are on the whole of greater scientific interest than of economic importance. The fungi (*q.v.*) are by far the most important group of disease-producing organisms, so far as plants are concerned.

Broadly speaking, therefore, the plant pathologist is by training either an entomologist or a mycologist. As far as diseases of parasitic type are concerned, only those caused by plants, and therefore chiefly of fungal origin, will be dealt with in the present article. At the same time it is important to note that the two aspects of the study of plant disease, the entomological and the mycological, cannot in practice always be separated.

**Symptoms of Disease.**—The study of symptoms is the first step in the examination of a disease problem. By symptoms one means the total of the modifications shown in the plant as the result of disease. In the majority of plant diseases of parasitic type the true symptoms are accompanied at one stage or other of the disease by certain appearances such as the fructifications of the parasite.

A very important difference between the typical plant disease and the typical animal disease is as regards the definiteness of the symptoms shown. In animals and especially in man disease symptoms are usually very characteristic, so that it is often possible to identify (or *diagnose*) a particular disease from a study of the symptoms alone. With plants this is not generally possible. Disease symptoms in the latter are much more generalized, *i.e.*, the same or approximately the same symptoms can be produced by a great variety of causes. Wilting of the foliage, for example, is a symptom of disease in plants and its cause may be most varied—damage to the roots by fungal or insect attack, damage to the stem, presence of injurious salts in the soil, scarcity of water, and so on. Hence it follows that while a study of the symptoms may give valuable indications of the nature of a particular plant disease, it is in general necessary to discover the cause or *aetiology* of the disease before the latter can be definitely identified. Determination of the causal agent may be difficult and usually involves considerable expense of labour and time.

While the main symptoms of plant disease are of a rather generalized nature, a number of different types may be distinguished. The more important of these are given in the following list:

(a) *Change of colour*, such as paleness, silvering, reddening, blackening of leaves. The change of colour may be shown over the leaf or even over the whole plant, or it may be limited to spots, streaks or patterns, such as the well-known “mosaic” appearance.

(b) *General wilting* of the shoot, as when the plant suffers from drought, or from “damping off” disease, or from the effects of a parasite which destroys the roots or is present in the water-conducting system.

(c) *Premature shedding* of leaves, blossoms, fruits, etc.

(d) *Abnormal retention* of leaves, which is especially well shown in certain diseases of deciduous trees. The autumnal shedding of leaves is a vital or physiological process, due to the action of a definite *absciss* or cutting-off layer at the base of the leaf. If this layer is prevented from functioning, as for example by the killing action of a parasite which has invaded it, the leaves cannot be shed in the normal way.

(e) *Dwarfing or stunting*, which may be general to the whole plant or may only be shown in particular organs.

(f) *Abnormal enlargement or multiplication* of parts (*hypertrophy*) resulting in the formation of such structures as galls, tumours, knots, warts, etc. (fig. 1). Hypertrophy is generally

accompanied by distortion or malformation as in the rolling or puckering of leaves and the twisting of shoots. Frequently it takes the form of an abnormal development of buds, the majority of which would normally have remained dormant. The structures called “witches’ brooms” (fig. 1) which are common on certain trees (*e.g.*, willow, birch) are produced in this way.

(g) *Replacement* of one organ by another, as for example the change of petals into foliage leaves. Some changes of this type, though properly speaking malformations, may be economically desirable and are therefore not considered as diseases. An example is the “doubleness” of some flowers.

(h) *Change of habit of growth*, *e.g.*, from the prostrate to the erect, from the climbing to the non-climbing type of growth (fig. 1).

(i) *Change in the periodicity relationships* of the plant, as for example the premature flowering (“bolting”) of a biennial plant in its first year of growth, or the opening of foliage or floral buds at the wrong time of year.

(j) *Replacement* of parts of the plant by structures belonging to the parasite, such as the conversion of the rye grain into the resting organ (*sclerotium*) of the Ergot fungus (fig. 1). “Mummification” of certain fruits is another example of this type.

(k) More or less rapid *killing* (*necrosis*) of the plant or parts of it. Killing is often accompanied by more or less pronounced rotting, as in the decay of fruits, buds, etc. (fig. 1). Localized killing of leaves results in the formation of dead spots. The killed tissue may remain as such or may dry up and fall out, thereby producing a “shot-hole” effect.

(l) Formation of *deep-seated wounds* or *cankers* (fig. 1). In a canker, the parasite slowly eats into the plant tissue, the part invaded being killed and to a large extent disappearing. Associated with this type of wound there is usually a certain amount of hypertrophy of the tissue which still remains alive round the margin of the invaded part.

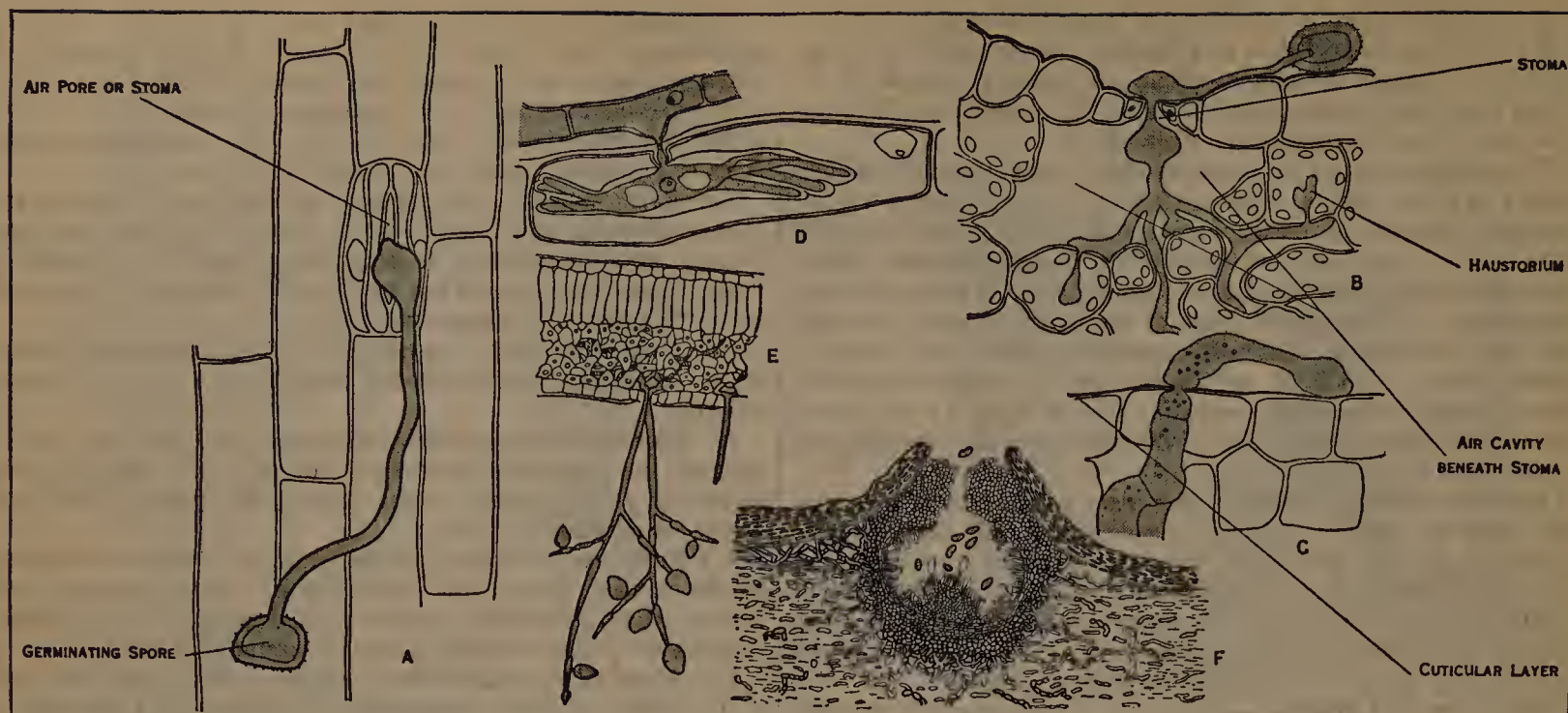
(m) Various kinds of *exudations*, as in the gumming of plum trees or the abnormal flow of resin in certain conifers.

#### METHOD OF STUDYING PLANT DISEASE

Though the investigation of a plant disease is a matter for the specialist, a short account of the methods adopted will serve to indicate the type of problems encountered. The parasitic type of disease is in practice the one most frequently met with, and therefore in actual study it is usually assumed in the first instance that the disease under investigation is of parasitic origin.

**Identification of the Parasite.**—The first problem which arises is the determination of the nature of the parasite (assuming that such is actually present). The tissues of the plant which show the symptoms of disease are examined, after suitable preparation, under the microscope and if the disease is actually due to a parasite it is usually not difficult to demonstrate its presence. Definite indications of its nature and identity may also be obtained at this stage. In a number of cases, the parts of the plant which show the symptoms of disease may appear to contain no parasite, even though further study may confirm that the particular disease is of truly parasitic nature. Thus the parasite may be so small as to be beyond the range of microscopic vision (*see* Virus diseases, below), or, as occasionally happens, the parasite is located elsewhere but is able to produce symptoms in parts of the plant remote from it. The mere presence of a fungus or bacterium within the diseased part (or *lesion*) is not, however, a certain indication that the disease is caused in that way. Direct proof can only be obtained by inoculating healthy plants of the species showing the disease with the organism in question and observing whether the disease is thereby produced. The details of the procedure involved in the carrying out of such artificial inoculations will vary much in different cases. In general it is necessary, as a first step, to prepare “pure cultures” of the organism, that is, to grow the latter in such a way that no other organism is present. These pure or unmixed cultures of the organism are then tested separately by inoculations on the host plant, and by this means evidence is obtained as to which is the active parasite concerned. The active parasite being isolated and its pathogenicity





FROM (A) PHILOSOPHICAL TRANSACTIONS, BY COURTESY OF THE ROYAL SOCIETY, (B, C) ANNALS OF BOTANY, (D) BOTANICAL GAZETTE (UNIVERSITY OF CHICAGO PRESS), (E, F) DUGGAR, "FUNGUS DISEASES OF PLANTS" (GINN & CO.)

FIG. 2.—THE FINER STRUCTURE OF SOME PARASITIC FUNGI (MAGNIFIED)

A. Surface view of plant leaf, showing rust spore germinating, B. Section of leaf showing entrance of rust fungus through a stoma, C. Penetration of cuticular layer of plant by fungus, D. Haustorium or abortive process of mildew within plant cell, E. Fructification of potato blight fungus with egg-shaped spores, F. Fructification of Black Rot fungus embedded in the tissue of an apple, rupturing outer skin of the fruit

(or capacity to produce disease) proved, one is now able to identify the particular disease in terms of the parasite which is responsible for it.

Identification of the disease is of value inasmuch as it enables the investigator to correlate his work with similar work done elsewhere, and of which a record is obtainable in the scientific literature. But mere identification is not the most important part of the study. It is essential to work out the *life-history* of the fungus—i.e., to know where and in what form it occurs throughout the year. The same fungus may exist in a variety of forms in different situations or at different times of the year, and it is essential to connect up the various stages. In particular it is very important to establish the manner in which the fungus passes the winter (or equivalent) season. In temperate climates, for example, a summer growing season alternates with a period of dormancy during the winter. Often it is only on the actively growing crop in summer that the disease is observable. It reappears each spring, spreads during the summer, and becomes more or less latent during winter. The considerations which arise in this connection vary much in the different cases. A few examples will illustrate this. Annual crops pass the winter season in the form of seed. Is the disease therefore carried over the winter by means of the seed, and if so is it present within the seed, or is it carried on the surface? Or does it persist in the soil, or is the new crop infected afresh from dead remains (stubble, trash, etc.) of the preceding year's crop? Or again, do various perennial plants, such as certain weeds, serve to carry the disease through the winter? With perennial crop plants such as fruit trees, there is the further possibility that the disease may overwinter in a resting form on or in the plant itself. The determination of the exact method of overwintering which obtains in any particular case is obviously of the greatest practical importance.

The further examination of a disease problem from the point of view of the parasite would take into consideration the geographical range of the latter. Plants showing the particular symptoms would be obtained from different localities and the parasites isolated and compared. Thus a general idea would be obtained of the geographical distribution of the parasite and of the range of host plants which it could parasitize.

The complete elucidation of a plant disease involves much more, however, than the determination of the existence and habits of a parasite as outlined above. The presence of the parasite is only one of the conditions essential for the appearance of a

specific parasitic disease. The more important factors and the manner in which they operate will now be indicated.

**Temperature.**—First as regards temperature. This factor determines in large measure the rate of growth and general vigour both of parasite and host. There is a certain temperature (*minimum*) below which an organism will not grow, a *maximum* above which it will not grow, and an *optimum* at which it grows best. These three temperatures constitute the so-called *cardinal points* for the particular organism. The cardinal points for the parasite are not in general the same as for the host plant, and the cardinal points for the disease itself are not the same as those of either host or parasite. Usually the range of temperature over which disease takes place is distinctly narrower than that over which either of the two organisms concerned will grow. The optimum temperature is well known in many cases to be different for host and parasite, and thus it is clear that the possibility exists of finding a temperature at which the host plant grows well but which is unfavourable for the development of the disease. The precise relationships are somewhat complex and have been fully worked out for a limited number of diseases only, but it is possible in general terms to classify diseases into the two main types, high temperature and low temperature diseases. An example of each will show the difference. The root-rot disease of tobacco is one of the low temperature type. Susceptible varieties of tobacco when grown in infected soil are badly diseased if the temperature runs low, whereas in the same soil the disease would not occur at a higher temperature. The wilt disease of cabbage is of the high temperature type, and only occurs in seasons when the general ground temperature is high.

**Water.**—The water-relationships of the crop are of equal importance with those of temperature and are to be studied in terms of the amount and distribution of rainfall, the water-retaining capacity of the soil, drainage, etc. Two factors which are of great importance in the initiation of parasitic attack are the relative humidity of the air surrounding the plant and the percentage of moisture present in the soil. The parasite requires the presence of a certain amount of moisture to start its growth processes. So it will often be possible for the plant pathologist to explain the occurrence of disease at one time or place and not at another in terms of these factors. The percentage of moisture in the soil affects not only the capacity of the parasite to grow but also the growth of the roots of the plant. It may therefore also influence the capacity of the roots to resist the attacks of



the parasite.

**Light.**—Light is also a factor which influences the susceptibility of a plant to disease. The quantity of light received by the plant determines in large measure its vigour of growth, not merely as regards the amount of new tissue formed, but also as regards the mechanical strength and to a certain extent the chemical composition of the tissues of the plant. These qualitative differences influence the degree of resistance which the plant can offer to the attack of a parasite. For example the weak, pale, rather juicy, "forced" type of growth which results when plants are grown under conditions of feeble illumination—as when plants are grown in glasshouses during winter or when they shade each other by standing too closely together—predisposes them to attack by a variety of fungi ("damping-off" diseases). On the other hand, certain fungi (*e.g.*, some of the rusts) attack their hosts with vigour only when the latter are growing under conditions of good illumination. Again, the symptoms of certain diseases (*e.g.*, some mosaics) will only appear when the plant is exposed to light of a certain range of intensity.

The three fundamental factors, temperature, humidity and light are, in the open field, to a large extent beyond control. Nevertheless, it is often possible, in agricultural practice, materially to modify their action. By suitable methods of cultivation—draining, subsoiling, ridging, manuring—the amount of soil water can be regulated. By the provision of shade trees—as is usual in many tropical cultivations—or by suitable spacing of the crop itself or by pruning, the intensity of light or humidity of the air can be adjusted so as to approximate to the needs of the plant.

**Soil Factors.**—Reference has been made to soil moisture as a factor of importance in connection with plant diseases. This is merely one of the many soil factors which influence plant growth and which therefore require to be considered in dealing with the liability of plants to disease. The physical texture of the soil and the presence or absence of certain chemicals are of importance mainly inasmuch as they influence soil humidity. But there are in addition a number of soil factors which act otherwise. Thus the amount of certain constituents present in the soil (*e.g.*, nitrogen, potash, phosphate) influences not only the quantity of plant growth but also, to an appreciable degree, its quality—and in particular its susceptibility to disease. The presence or absence of lime, by controlling the reaction of the soil, is in some cases the factor which determines whether a particular disease will develop or not. Soil aeration is a factor in itself, though in practice it is often difficult to separate its effects from those due to soil humidity.

**Internal Factors.**—So far the discussion of the factors which influence plant disease has been limited to the environment. The latter, however, merely modifies the result which is in the main conditioned by the structure and physiology of the host plant itself. These "internal" factors are more elusive than those already discussed and in their fundamental aspects are practically unmapped. A few examples of internal factors and of their manner of functioning will be given in the following section. Nevertheless, though very little is known of the underlying factors which determine immunity or susceptibility, certain phases of the problem are open to direct observation and experiment.

From the foregoing sketch it is clear that the complete investigation of a plant disease may ramify into various branches of agricultural science. The plant pathologist is thus much more than a mycologist, or student of fungi, though in practice the two names are often used as equivalent. Plant disease investigations may call for the joint work of the mycologist (or entomologist), the soil chemist, the physicist and the practical agriculturalist, and lastly—as will be shown more clearly later—the co-operation is required of the geneticist for the breeding of resistant varieties, and of the pure chemist for the preparation of chemical means of combating the disease.

#### NATURE OF DISEASE; PHYSIOLOGY OF PARASITISM

The discussion under this heading will be confined almost wholly to diseases of parasitic nature. The problems presented in parasitic disease are simpler inasmuch as the interactions of

parasite and host plant can be studied under the microscope, and to a certain extent at least are amenable to chemical and physical analysis. For simplicity, the description will be confined to a disease of fungal origin.

The earliest phase of such a disease is the entrance of a fungal thread or *hypha* (*see FUNGI* for account of fungal structure). The fungus, usually in the form of a spore, germinates on the surface of the plant, or otherwise comes in contact with the latter. It then enters, either by naturally occurring openings (stomata, water pores) (*fig. 2*) on the surface or by boring directly through the skin or cuticle of the plant (*fig. 2*). Certain parasites, known as *wound parasites*, are only able to enter through openings or wounds which have been made by other agencies; *e.g.*, insect bites, bruises due to processes of cultivation, frost cracks, wind damage, pruning wounds, etc. Then again dispute exists as to whether the actual process of penetration is effected by purely mechanical means or by the agency of some chemical substance which softens or dissolves the cuticular layer of the plant. Once inside the plant, the fungus progresses by sending hyphae through the tissue, either between the cells (*intercellular*) or into the cells (*intracellular*). The particular relationship shown—*i.e.*, whether the hyphae are *between* or *actually in* the host cells—is more or less characteristic of individual diseases. In many cases the hyphae of the fungus ramify between the cells of the host and here and there send characteristic outgrowths (*haustoria*) into the cells themselves (*fig. 2*). These outgrowths are clearly the organs which enable the parasite to abstract its nutriment from the host cells.

While the fungus is progressing through the plant, the cells of the latter in the neighbourhood of the parasite, or even at some distance from it, show a number of more or less characteristic changes. The total sum of these changes, it should be noted, constitute the symptoms of the disease. The details of the changes shown vary much from one disease to another, but broadly speaking one can distinguish two main types of disease, each with a characteristic set of host changes associated with it.

**Generalized Parasites.**—In the first type, the fungus pours out certain chemical substances into the surrounding host cells, with markedly destructive effects to the latter. The living contents (*protoplasts*) of the cells are killed and the walls which separate the individual cells (and which form the mechanical skeleton of the living plant) are softened or partially dissolved. The destructive principle exuded by the fungus is able to diffuse out into the host tissue and thus bring about killing of the latter well ahead of the growth of the fungus. Fungi of this type are therefore not parasites in the strict sense of the term, inasmuch as they are growing all the time, not on the living plant, but on parts of it they have previously killed.

This type of parasitism is relatively simple and crude. The fungus, so to speak, is in the nature of an assassin who kills and then plunders his victim. The essential part is the killing and this merely entails that the fungus must possess the necessary battery of substances for carrying out this process. In these respects such fungi and the diseases to which they give rise stand in marked contrast to the type which will now be described.

**Specialized Parasites.**—In the second type of disease, there is no rapid killing or rotting effect produced by the parasite on the host cells in the neighbourhood. The cells of host plant and parasite live side by side for a considerable time with no apparent damage to the former. Indeed it frequently happens that the presence of the parasite stimulates the host cells to unusual growth and activity. Thus the cells in the neighbourhood of the parasite, some of which are actually penetrated by the food-absorbing processes of the latter, are often found on examination to be more richly supplied with food reserves than are the normal cells removed from the zone of influence. If the part of the plant affected is a leaf or other green part, the stimulating effect produced by the parasite may often be seen in the more intense green round the margin of the invaded spot than elsewhere. The stimulating action in many cases takes the form of renewed growth on the part of cells which normally would not have grown further. In this way are produced the tumours, galls, warts, witches'



brooms, etc., frequently associated with diseases of this type. Such parasitism illustrates the *symbiotic* relationship to which reference has already been made. The symbiotic relationship may persist for a considerable time, but by and by injurious effects supervene, leading to more or less extensive destruction of the host tissue.

The second type of parasitism is much more subtle in nature than the first. The method of attack adopted has no resemblance to that of the assassin but savours rather of the blackmailer whose interests would not be well served by the premature death of his victim. Up to a point the interests of blackmailer and victim are identical, and if the association leads to unusual industry on the part of the latter the final harvest is all the richer. In diseases of the second type an analogous behaviour is shown. The analogy can in fact be pressed more closely still. Fungi which produce the first type of disease are, like the assassin, not selective in their action. In diseases of the second type, on the other hand, a high degree of selectivity is typically shown.

Fungi which produce this specialized type of disease show specialization in other respects. Their food requirements are of a very particular nature, and on this account it is generally impossible to cultivate them on any medium other than the living plant to which they are specialized. The symbiotic relationship is apparently necessary, and if this is not developed, no effective parasitism ensues.

As fungal attack progresses, one usually finds that the parasite makes provision for its further distribution by the development of a fruiting or sporing stage. The spores may be formed within the tissue of the parasitized plant and are disseminated only when the latter is decomposed, as for example by rotting on the surface of the soil. More generally the fructifications of the fungus are developed on or towards the outside of the plant, either emerging from the stomata or bursting through the outer skin (fig. 2). Many fungal parasites develop two kinds of spore. One of these is produced in profusion during the growing period and serves to spread the disease rapidly to new plants. This is the so-called summer spore, which is usually short-lived and germinates with great readiness when the environmental conditions are suitable. The second type of spore is usually produced later in the season. This is a resting form which typically will not germinate until after a certain interval has elapsed, and which in some cases requires exposure to winter cold before it is capable of germination. The resting spore is usually provided with a thick protective wall, and is capable of enduring long exposure to atmospheric conditions. Its function is to carry the fungus over the winter.

**Immunity.**—The preceding sketch of the progress of a successful parasitic attack would be incomplete without some reference to those features of the plant which confer resistance or immunity to disease. These are the “internal” (as apart from environmental) factors to which reference was made above. It was also pointed out that immunity to certain highly specialized fungi was really due to over-susceptibility.

It may be noted in the first instance that a plant may be immune in the practical sense for the reason that it merely *escapes* disease. Internally it may be just as susceptible as other plants which become badly diseased. The presence of water-drops on the surface, which enable germination of the fungal spores, is a necessary antecedent to attack. Many plants are enabled to escape attack on account of a property of their outer surface which prevents the adherence of water.

With fungi which penetrate the cuticle, the strength of the latter is obviously of importance, at least if the mechanical view of penetration is accepted. In many cases there is definite evidence that this factor comes into play. Thus certain fungi are only able to attack the young leaves in which a mature, fully thickened cuticle is not yet present.

When the fungus has actually entered the tissues of the plant, it must, if parasitism is to be effected, be able to live in the sap with which it comes into contact. Attempts have therefore been made to explain the susceptibility or resistance of a tissue in terms of the properties of the plant juices. Certain difficulties of a technical nature are met with in such investigations; *e.g.*, it is not certain how far an extract which is pressed out from a

plant is a true representation of the cell-sap originally present in the cells. Up to the present it has been possible only in a few cases to correlate the resistance of the host tissue to fungal attack with the anti-fungal properties of the plant juice.

The method by which the “killing” type of fungus breaks down the resistance of the host tissue is by excreting certain enzymes which partially dissolve the cell walls and kill the protoplast. These ferments are highly specific in action; *i.e.*, they are active on some tissues and not on others. The main factor in this connection seems to be the chemical composition of the cell walls.

So far we have dealt with possible chemical measures of defence. Many plants adopt a mechanical means of defence by laying down a protective layer of cork in advance of the parasite. The corking-over of an exposed or wounded surface is a common reaction of plants, and the same often takes place in response to the wound caused by a parasite. One or more layers of corky cells are formed somewhere along the line of separation between diseased and healthy tissue, and these act as a mechanical barrier to further progress. Any condition of the invaded plant which tends to accelerate this formation of cork increases the resistance to attack, and conversely. Similarly it has been shown in one case (the “silver leaf” disease of plum trees) that resistance depends on the formation, as a wound response, of a layer of hard gum which mechanically shuts off the parasite.

No reliable evidence exists as yet of any formation of antibodies such as play a fundamental part in the arrest of certain animal diseases. Here we meet with another illustration of the essential difference between plant and animal diseases.

#### ECONOMIC IMPORTANCE OF PLANT DISEASES

The number of known plant diseases is very great, and even if those occurring on non-economic plants are ignored, there is still a large residue. A glance at the disease lists of economic crops, such as are published from time to time by departments of agriculture and other bodies, will show as many as twenty or more diseases occurring on particular species of cultivated plants. The majority of these appear, for the present at any rate, to be of little economic importance, but one may say generally that more or less all cultivated plants are subject to two or three diseases of major importance, which at various times or places interfere seriously with their profitable cultivation. Thus in the case of the potato, one may cite four important diseases, blight, wart, common scab and virus disease, all of which afford serious problems to the grower. Of the many diseases reported on the apple, one may mention mildew, scab, canker, brown rot, bitter pit and scald as of the greatest economic importance; and so on, for other crop plants. In any one year and in a given locality, certain of these diseases may do little damage or may even appear to be absent, but over a wide area and over a period of years the aggregate loss is very great. One might forecast that the seriousness of the losses due to plant disease will tend to become greater as the gradual increase in the world's population makes it less possible for the supply of any product to outstrip the demand.

Though the farming class as a whole may in certain cases reap an advantage from the prevalence of plant disease, to the individual farmer the occurrence of disease in his crops can only bring loss. He therefore adopts certain measures with a view to protecting his crops and submits to various legislative restrictions, the object of which is to prevent or limit the spread of plant diseases. All these measures have as their ultimate result an increased cost of production of the article concerned, and this in the long run represents a loss to the community.

**Epidemics.**—It is, however, when plant disease comes on in epidemic form that the most striking damage is produced. The general public which is unaware of the widespread and ever-continuous frittering away of plant products as a result of disease, sees then the disease in its most concentrated form. Such epidemics have at one time or other produced enormous losses. They have profoundly influenced the economic development of certain countries, and have led frequently to acute distress and famine. The following examples will serve to illustrate these statements.

The rust diseases of cereals are present in all cereal-producing



countries and the annual loss in many of them runs into millions of pounds sterling. The estimated loss from the stem-rust disease of wheat in 13 of the northern United States for the ten-year period 1915-24 is given as about 550 million dollars, half of which loss was incurred in a single "rust" year, 1916. The rust epidemic of 1891 cost Prussia about three-quarters of the whole cereal crop. Similar disasters have occurred in India, Australia, South Africa and other wheat-growing countries. It is simply the fact that wheat is cultivated in so many widely separated countries—in all of which a rust epidemic is not liable to occur in any one year—which acts as a safeguard against a serious bread famine.

The coffee disease, also caused by a rust, is a striking example of the effect which a disease may have on the economic history of a country. In the earlier part of the second half of the 19th century, the coffee industry was the mainstay of the prosperity of Ceylon. About 1870 a hitherto unrecorded leaf disease appeared on the coffee bushes. As with many important plant parasites, the seriousness of this disease was not recognized at first. Within a few years the fungus had spread over the whole island and the coffee industry soon disappeared from Ceylon.

Perhaps the most outstanding instance of distress caused by a fungal disease is afforded by the great Irish potato famine in 1845 and 1846. The potato disease ("blight") had only appeared in Europe a few years previously, the causal fungus being, like the potato itself, a native of South America. The disease spread like wildfire over western Europe and in the seasons 1845 and 1846 almost completely destroyed the potato crop in Ireland. As the potato at that time constituted the staple food of the peasant population, the result of the epidemic was a famine of unprecedented severity.

The story of the coffee leaf disease in Ceylon has in recent years found a very close parallel in that of the chestnut blight in the United States. This disease first appeared in 1904 on a few trees in the neighbourhood of New York. Subsequent investigation showed that the causal fungus was a native of Eastern Asia where it occurs on certain native species of chestnut, but without causing appreciable damage. It had apparently been introduced into the United States on a consignment of chestnuts from the East, and there is every probability that if its importance had been recognized, the disease could have been stamped out in the early stages. As it was, the disease began to spread over the New England States and it soon became apparent that the fungus was much more destructive to the American sweet chestnut (*Castanea dentata*) than to the Asiatic forms. Control methods of the most elaborate nature were put in operation, but too late to be effective. At the present time, this disease has destroyed practically all the native chestnuts in the United States. (See CHESTNUT.)

Records of the complete extermination of an industry by fungal disease are fortunately not numerous. On the other hand it would be possible to multiply examples in which fungal diseases are an ever-present menace to particular cultivations. The most important single factor in the cultivation of many economic plants is the liability to certain fungal diseases.

#### METHODS OF CONTROLLING PLANT DISEASE

The checking of a plant disease, so that if not actually eliminated it is reduced to manageable proportions, is spoken of as its "control." This may be complete or partial. The methods of control may be divided into two main groups, first those which are put into practice by the grower himself, and second those which are enforced upon him by legislation. In the following discussion these will be considered separately.

**Voluntary Control.**—The adoption of control measures by the grower is subject to a number of severe restrictions. It is only with a certain number of crops that individual treatment of plants is possible, and in all but exceptional cases the economic consideration of cost is all-important. It is idle for the plant pathologist to suggest measures of control if the requirements of time and labour involved in the treatment are such as cannot be satisfied or if the ultimate gain to the grower is not obviously

greater than the cost of the measures adopted. The control methods adopted may be directed to increasing the resistance of the plant to disease, or in the case of a parasitic disease may also be directed against the parasite. The former will be dealt with first.

**Resistance.**—For every plant there is a certain range of environmental conditions within which it grows best. If the conditions vary widely in any important respect from those which are ideal, the plant grows badly. A weakly growing plant is in general more susceptible to parasitic attack than is a strongly growing one, and the abnormal condition of the plant resulting from the unfavourable environment may in itself be so pronounced as to be called diseased. Good cultivation, therefore, which aims at giving the plant the optimal conditions for its growth, is the first line of treatment to be adopted with a view to lessening the incidence of disease.

The most approved methods of husbandry will not however guarantee freedom from plant diseases, nor are they always practicable. More special methods must therefore be adopted. In recent years it has become increasingly recognized that the main line of defence against many important diseases consists in the development of *immune* or *resistant varieties* of the host plant.

To obtain varieties of a crop plant which are resistant to a particular disease is in many cases not difficult. These may in fact exist among the varieties already in cultivation. If the resistant forms possess high merits in other respects—*e.g.*, in yielding power, in quality of product, etc.—then the problem of the particular disease is in large measure solved. Often, however, the resistant varieties which are already known to occur show certain disadvantageous features, and these may be so great as to outweigh the benefits conferred by the high disease resistance shown.

One method of obtaining a resistant *strain* from a commercial variety consists in growing the plants under conditions in which they are exposed to infection and selecting out for propagation those individuals which stand up successfully against the disease. This method has been adopted with great success in the development of strains resistant to some of the important wilt diseases (cotton, cabbage, etc.).

A more elaborate method consists in the artificial crossing of parents of known characteristics, followed by the sorting out of the different types which occur among the progeny. (See PLANT BREEDING.) This is the application to problems of disease of the principles of Mendelism (*q.v.*). Resistance to disease behaves as a single or multiple Mendelian factor, and is usually dominant in the immediate offspring.

**Destruction of the Parasite.**—The control of plant diseases by the adoption of measures against the fungus is best considered with reference to the life-history of the fungus and in particular to the manner in which it reinfects the growing crop after each period of winter dormancy.

If the fungus is a *soil parasite*, it may be possible to starve it out by ensuring that it does not come in contact with the particular crops on which it grows and multiplies. This involves a system of *rotation* of crops. The practice of crop rotation is justified for other agricultural reasons and is of great value in that it tends to check the multiplication of specific soil (and other) parasites. Some soil parasites however are able to live indefinitely on the humus material of the soil so that they cannot be starved out (*e.g.*, some wilt diseases), others may persist so long in the dormant form that the interval required between successive susceptible crops is too long to be economically practicable (*e.g.*, wart disease of potato).

The elimination of a parasite from the soil by any process of sterilization is generally impracticable on account of the expense involved. In greenhouse cultivation or in those cases where the main source of infection is the seed-bed, soil sterilization may be attempted. For this purpose, heat (*e.g.*, steam-heat as obtained from a boiler) or a fungicidal chemical such as formalin is generally used.

**Preventive Measures.**—If the disease is carried by the seed,



the practical method of control consists either in the selection of seed known to be free from contamination or in some process of seed treatment devised to destroy the parasite without appreciably affecting the germinating capacity of the seed. If the fungus is present merely on the surface of the seed, treatment is generally simple. This consists in steeping the contaminated seed in solutions of various chemicals—formalin, copper sulphate, mercuric chloride, organic salts of mercury, etc.—for a suitable time. The fungus is killed by this treatment whereas the seed is little damaged on account of the protection afforded by its seed coat. Dusting the seed with various chemical powders is similarly effective.

A general palliative measure in the treatment of plant disease is to reduce the amount of infective material available. If the fungus overwinters on the dead remains of the previous year's crop, the latter should be disposed of, either by burning or by digging into the ground. Crop rotation, by segregating to some extent the current year's crop from last year's, is likewise useful.

One of the most important methods of protecting plants against the attack of air-borne parasites is by the use of fungicidal chemicals which are sprayed or dusted over the plants. The object aimed at here is to coat the surface of the plant with a thin but more or less continuous film of the fungicidal substance so that, when the air-borne spores of the parasite arrive, they are unable to initiate attack. Spraying or dusting, if properly carried out, prevents attack but is ineffective if the disease has already established itself. Thus an intimate knowledge of the life-history of the fungus with special reference to the date at which it emerges from its winter resting stage is of the greatest importance for success in spraying operations. The leaves and young shoots of the plant are readily injured by the action of poisonous chemicals, so that great care is necessary in the preparation and use of fungicides, otherwise greater damage may be done than that which it is intended to prevent. The spray, which consists of a very fine suspension in water of the fungicidal substance, is discharged under pressure in the form of a mist so that as far as possible the whole plant surface is covered. In practice various inert substances ("spreaders") are added in order to facilitate wetting of the leaves and adhesion of the spray. The basis of most sprays in commercial use is either copper or sulphur. To the former class belong the well known Bordeaux and Burgundy mixtures, prepared by adding solutions of copper sulphate to lime and soda respectively. To the latter belong such preparations as "liver of sulphur," "lime sulphur" and "colloidal sulphur."

**Legislative Control.**—The legislative enforcement of certain measures for the control of plant diseases actually dates back for several hundred years. Witness for example the Rouen act of 1660 for the control of wheat rust by the eradication of barberry bushes (*see later*). The full development of these measures however has only come about within the last twenty years. The Destructive Insects and Pests Act was passed by the British parliament in 1907 and a similar law, the National Plant Quarantine Act came into force in the United States in 1912. Practically all civilized countries adopted the same type of regulations and at much the same time.

**Restriction of Imports.**—As between one country and another, the effect of these enactments is to limit free trading in such plants or plant products as are considered likely to bring dangerous parasites into the importing country. The restrictions may amount to a complete embargo, as applies for instance to the import of English potatoes into the United States (on account of the wart disease) or of American gooseberry bushes into England (on account of mildew). In other cases import is allowed provided the material has been inspected by a responsible authority in the exporting country and warranted free from certain diseases. Such material is subjected to further inspection at the port of entry and if found contaminated may be destroyed. From the port it may be liberated directly to the trade or may be sent to a quarantine station, where it is grown in an isolated situation for such time as enables its freedom from disease to be fully established. These restrictive regulations may also be in force between

different parts of the same country, as for instance, between the different states of the United States.

**Domestic Control Measures.**—Within the limits of any one country, legislative control may take the form of compulsory notification of certain diseases. The latter will then be inspected, and the appropriate measures—such as destruction of the infected material—enforced. A further measure is the placing of restrictions on the kind of crop which may be grown within certain infected areas. The legislation against wart disease of potato in England is an illustration of this type of control measure. Within an infected area (called a "scheduled" area) only immune varieties of potatoes may be grown. The enforcement of this kind of measure is very difficult unless suitable immune varieties or other substitute crops are available.

Legislative control of the type outlined above has naturally led to the creation of an inspection service, and further to a wide extension of facilities for advisory work and for the carrying out of research. This increased interest in problems of plant disease, arising from government intervention, is perhaps the most striking development in plant pathology which the 20th century has produced.

### CLASSIFICATION OF PLANT DISEASES AND SPECIAL ACCOUNT

In the present section a brief account will be given of some of the more important plant diseases and under the following headings—

- (a) Physiological Plant Diseases.
- (b) Plant Diseases due to Bacteria.
- (c) Plant Diseases due to Viruses.
- (d) Plant Diseases due to Fungi and Slime-Fungi.
- (e) Plant Diseases due to Higher Plants.

**Physiological Plant Diseases.**—Plants, like animals, may show deficiency diseases due to the lack of some important chemical constituent in their food supply. Thus a lack of iron salts in the soil produces the condition called "chlorosis," in which the green pigment of the plant, chlorophyll, fails to develop. Lack of potash, such as often occurs in poorly manured soils or in light soils leached by heavy rainfall, produces very characteristic symptoms of disease in certain plants, *e.g.*, potato, tobacco and cereals. Similarly for other essential food elements such as magnesium, phosphate and nitrogen. Conversely disease conditions may result from the presence of an excess of certain chemicals in the soil. To this class belong various kinds of chlorosis, due to excess of lime or manganese in the soil. The most important diseases of this type are those associated with the accumulation of soil alkali. These are met with in irrigated regions where they often constitute the chief agricultural problem.

Among diseases due to unsuitable environmental conditions may be cited those caused by too high temperature, such as sunscorch of leaves, heat canker, etc. The effects of too low temperature are familiar as frost injury to leaves, young shoots, fruit, etc., but a more important illustration is seen in the winter killing of trees in those countries which experience severe winter freezing. The development of "winter-hardy" varieties of cultivated plants is of great importance in countries possessing the continental type of climate.

Injuries due to noxious chemicals in the air are well shown by plants growing in industrial areas. The more important chemicals in this connection are gases, such as coal gas and sulphur dioxide, fumes such as sulphuric acid, and dusts such as soot and cement dust. The latter act by choking up the breathing pores of the plants, but this action is often accompanied by the poisonous effects of gases associated with the dust. In this connection should also be mentioned the injuries which arise from the injudicious use of chemical protective agents such as sprays.

**Plant Diseases Due to Bacteria.**—The most important diseases of this type are the fire blight (*Bacillus amylovorus*) of apples, pears and similar fruits; the angular leaf spot or black-arm disease of cotton (*Pseudomonas malvacearum*); the olive tubercle (*P. Savastanoi*); citrus canker (*P. citri*); various wilt diseases (*Bacillus tracheiphilus* in cucurbits, *B. solanacearum* in



tomato, potato, etc.); soft rots of a number of vegetables (*B. carotovorus* and allied species); two leaf spot diseases of tobacco (*Bacterium angulatum* and *B. tabaci*); and crown gall (*P. tumefaciens*) on a large variety of herbaceous and woody plants.

**Plant Diseases Due to Viruses.**—This important group was formerly placed among the physiological diseases, but it is now known that they are of infectious or contagious nature. Detailed investigation has failed to show the presence of a visible parasite, but in other respects the resemblance to the parasitic type of disease is very close. The disease can in many cases be transmitted by the inoculation of the juice of a diseased plant into a healthy one. Where this simple method of transmission fails, infection of a healthy plant can be obtained by grafting on it a shoot of a diseased plant. In certain cases it has been proved that the juice of a diseased plant is able to convey infection after it has been filtered through a porcelain cup, whence the current view with regard to these diseases is that they are caused by filter-passing organisms. The symptoms of virus disease are confined to the shoot portions of the plant, and take the form typically of mottling ("mosaic") of the leaves, with as a rule a certain amount of puckering, distortion or inrolling. The habit of growth may also be affected, and often there is dwarfing, premature death, and a marked diminution in the yield. The chief agents of transmission are various leaf-biting or leaf-sucking insects, particularly aphides. The number of crop plants which are known to show virus diseases is very large and includes potato, tomato, tobacco, cucumber, clovers, spinach, hop, sugar cane, sugar beet, peach and many others. Certain kinds of ornamental variegation are also infectious and are thus not distinguishable from virus disease.

**Diseases Due to Fungi and Slime-fungi.**—These constitute by far the most numerous group of plant diseases. The species of fungi which cause plant disease are to be numbered by thousands and occur in all the main divisions into which fungi are classified (see FUNGI). In the majority of text books on plant pathology, these diseases are classified according to the systematic relationship of the causal fungus, but in some cases a grouping according to the crop plant affected or according to the type of symptom produced may offer certain advantages. In the present article, any systematic review of even the more important diseases is impossible. All that can be attempted is to indicate some of the more important groups or types.

The Slime-Fungi (*Myxomycetes*) are responsible for a few diseases of economic importance. The best known example is the finger-and-toe or club root of crucifers (turnip, swede, cabbage, etc.) due to the organism *Plasmodiophora brassicae*. This disease is remarkable for the large size of the hypertrophies produced on the roots of the affected plants.

The group of the Lower Fungi (*Phycomycetes*) includes two important disease-producing families. The more important of these is the *Peronospora* family or downy mildews which cause important diseases of a great number of crops, potato, vine, hop, lettuce, several grasses and many others. The downy mildew of the potato (*Phytophthora infestans*) produces the most important disease of all, the potato blight, to which reference has already been made. Many seedling diseases ("damping off") also belong here. The most important member of the second family is the organism *Synchytrium endobioticum*, the cause of the black scab or wart disease of potato.

Within the group of the *Ascomycetes* there are numerous important parasites. Species of *Sclerotinia* produce the brown-rot or "mummy" diseases of apple, plum and similar fruits, being among the most destructive orchard parasites. The family of the *Erysiphaceae* comprises the powdery mildews. These fungi cause the abundant formation on the plant of a powdery mass of summer spores, whence the name of the group. Crops of economic importance which are attacked by powdery mildews include cereals, clover, vine, hop, gooseberry, strawberry, apple, rose and oak. Species of *Exoascus* produce the leaf-curl disease of peaches and almonds and a number of interesting if economically unimportant diseases such as witches' brooms on cherry and birch. To the group of *Ascomycetes* also belong such important diseases

as ergot of grasses (*Claviceps purpurea*), apple canker (*Nectria galligena*), wheat scab (*Gibberella saubinetii*), black knot of plum (*Plowrightia morbosa*), chestnut blight (*Endothia parasitica*), and apple scab (*Venturia inaequalis*). The group *Basidiomycetes* includes three families of parasites of very great economic importance: the smuts, the rusts and the bracket fungi.

The smuts (*Ustilagineae*) are a peculiar group of parasites which live almost wholly within the host plant and usually direct their attack to the developing flower and fruit. The latter in the typical case is converted into a black powdery mass of spores which constitute the "smutted" head so characteristic of this type of disease. The most important examples are met with among the grasses—viz., the loose and covered smuts of barley, wheat, oats, rye, rice, maize, etc.

The rusts (*Uredineae*) include perhaps the most important of all plant parasites. The cereal rusts (*Puccinia graminis* and allied forms) are the best known and economically the most serious, but important parasites occur on apple, plum, coffee, Weymouth pine, and many others, especially herbaceous plants. A striking feature in the life history of some of these rusts is that they pass from one host species to another. Thus some forms of the wheat rust parasite have a stage on the barberry; the Weymouth pine blister rust passes to various species of currant. The elimination of the so-called "alternate host" offers a means of control for certain of these rusts. Hence the "barberry eradication campaign" which is being actively prosecuted in certain wheat-growing countries.

The bracket fungi (*Polyporaceae*) are a group which attack living trees and timber. These are generally wound parasites which gain entrance through broken branches or other injuries, destroy the wood of the tree, and from time to time produce the well-known bracket-like fructifications on the surface. Species of *Polyporus* and *Fomes* attack a large variety of growing trees.

Diseases due to Imperfect Fungi make up an enormous and miscellaneous list, including such as the following: many fruit rots (*Botrytis*, *Penicillium*), wilts (*Fusarium*), stripe disease of cereals (*Helminthosporium*), and an almost infinite number of leaf, stem and fruit spots (*Phoma*, *Septoria*, *Gloeosporium*, etc.).

**Diseases Due to Higher Plants.**—Parasites of this type are of great botanical interest, but as a rule of little economic importance. Well known examples are the mistletoe (which is a semi-parasite only, being able to manufacture its carbonaceous food from the air by means of its green leaves) and the dodder or love vine. These attach themselves to and parasitize the stems of other plants.

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**WOOD.** In all classes of plants, including for instance ferns, more highly organized than mosses, wood occurs in all members of the plant and is continuous from the finest rootlets up the root and stem, into the leaves and flowers or the equivalents of these. Wood performs two functions in the plant's life: first, it serves for the transport of water and contained salts, absorbed by the roots, to parts where this "raw sap" is needed and especially to the leaves; secondly it gives mechanical strength to the plant.

In palms and bamboos the wood of the leaves is string-like in form and is confined to the nerves or veins; from these the strings extend into the trunk or stem, where they descend but join one another at intervals thus producing a more or less basket-like or loose loofah-like complex, which is embedded in the general mass of tissue composing the rest of the trunk. Thus it is this linked net-like complex of woody strings that corresponds to the solid mass of wood of a pine or oak.

Wood that has attained only slight thickness and accordingly cannot be termed timber, is nevertheless utilized, for instance in the form of thin branches and twigs to make besoms and baskets. Even when wood attains greater thickness it is not always timber,



since there are some woods so soft, so light in weight, and so weak that they have little or no value at all as structural material upon which there is a demand for strength: such wood, however, supplies means of flotation for fishing-nets and buoys, and for insulation, while the lightest of all are pith-like and are the materials of which sun-helmets are composed. Some of these hats are known as "solar topees," yet the word "solar" has no relation whatsoever to the sun as it is a perversion of the East Indian name, *solah*, of the aquatic plant producing this wood. (See also the article *TIMBER*.)

(P. G. M.)

**FLOWER**, a term popularly used for the blossom of a plant, and so by analogy for the finest part or aspect of anything. Here it is dealt with only botanically. The flower is characteristic of the highest group of plants—the flowering plants (Phanerogams)—and is the association of more or less leaf-like organs which are concerned with the production of the seed. In modern botany the group is often known as the seed-plants or Spermatophyta (see *ANGIOSPERMS* and *GYMNOSPERMS*). As the seed develops from the ovule, fertilised by the pollen, the essential structures for seed-production are the pollen-bearer or *stamen* and the ovule-bearer or *carpel*. In comparative morphology, these are known as sporophylls because they bear the microspores (pollen-grains), developed in the microsporangia (pollen-sacs) or the megaspore, contained in the megasporangium (ovule). In the more primitive gymnosperms (*q.v.*) the micro- or mega- sporophylls are generally associated in separate cones, to which the term "flower" has been applied. But it is to more definite and elaborate structures in the higher angiosperms (*q.v.*) that "flower" generally refers.

**Bracts.**—Flowers are produced from flower-buds in the axils of leaves called *bracts*; "bract" is properly restricted to the leaf from which the primary floral axis arises, while leaves which arise between the bract and the flower are *bracteoles*. Their arrangement is similar to that of foliage leaves. In many cases, bracts protect the young flower, but they are sometimes undeveloped, and usually fall off early. Sometimes, especially with bracteoles, no flower-buds arise in their axils. At the base of the general umbel in umbelliferous plants is often a whorl of bracts, the *general involucre*, while *partial involucres* or *involucels* are found at the base of the umbellules. In Compositae the involucre surrounds the heads of flowers (fig. 12). When bracts become united, the outer ones often do not produce flowers. A sheathing bract or *spathe*, enclosing one or several flowers is common among monocotyledons and may, in some palms, reach 20 ft. in length and enclose 200,000 flowers. The spathe may be coloured (*Anthurium*) or white (arum lily, *Zantedeschia ethiopica*). In grasses, the outer scales (glumes) of the spikelet are sterile bracts. Bracts may be changed into leaves (phyllody).

**Inflorescence.**—The arrangement of flowers on the axis is called the *inflorescence*. The primary axis of the inflorescence is the *rachis*; its branches, when present, are *peduncles*, which in turn may give rise to *pedicels*. A flower having a stalk is pedunculate or pedicellate; one with no stalk is sessile. To obviate any confusion, it is common to speak of the rachis as the *primary* floral axis, the peduncles as the *secondary* floral axes, and so on. The peduncle may be simple, bearing a single flower, or branched. When it proceeds from radical leaves, it is a *scape*. The floral axis may be shortened, as in daisy and fig, or flattened, convex or concave in form and bearing numerous flowers, as in marigold or in fig. Adhesions occasionally take place between the peduncle and the bracts, as in the lime-tree (fig. 1). The termination of the part upon which the whorls of the flower are arranged is the *receptacle*.

There are two types of inflorescence—one in which the flowers arise as lateral shoots from a primary axis, which goes on elongating, and the lateral shoots never exceed in their development the length of the primary axis beyond their point of origin; the flowers are thus *axillary* and the inflorescence is *indeterminate*. In the other type, the primary axis ends in a single flower, but lateral axes arise from the axils of bracts and repeat the process, the development of each lateral axis being stronger than that of the primary axis beyond its point of origin. The flowers are thus

*terminal* and the inflorescence is *definite*. In indeterminate inflorescences, the lower or outer flowers expand first (*centripetal*); in determinate inflorescences, it is the upper or inner flowers that open first (*centrifugal*). In some inflorescences (*mixed*), the primary axis has an arrangement belonging to one type, the branches one of the opposite type.

Amongst indefinite forms, the simplest is when a lateral shoot in the axil of a single foliage leaf ends in a single flower. In this case the flower is *solitary*. A more complicated inflorescence is commoner. Thus if the primary axis, as in fig. 2, is elongated and gives off pedicels ending in a single flower, a *raceme* is produced, which becomes a *panicle* if the secondary axes branch. If the lower flower-stalks are developed more strongly than the upper, and thus all the flowers are on a level, a *corymb* is formed, which may be simple (fig. 4) or branched. If the pedicels are wanting, so that the flowers are sessile, the result is a *spike*. If this bears unisexual flowers it is a *catkin*; if it becomes succulent and surrounded by a spathe it is a *spadix*, which may be simple (fig. 7) or branched. A spike with female flowers only and covered with scales, as in the hop, is a *strobilus*. In grasses there are usually numerous sessile flowers in small spikes (*spikelets*); if these are borne not on the primary but on secondary axes, they form a *panicle*.

If the primary axis is contracted, other forms result. When it is so short that the secondary axes arise from a common point and spread out as radii of nearly equal length each ending in a single flower or dividing again similarly, an *umbel* (fig. 8) is produced. If there are numerous flowers on a flattened, convex or concave receptacle, having short pedicels or none, a *capitulum* is formed, as in marigold and scabious (fig. 3). If the margins of the receptacle are developed upwards, they may ultimately give rise to the *hypanthodium* of the fig.

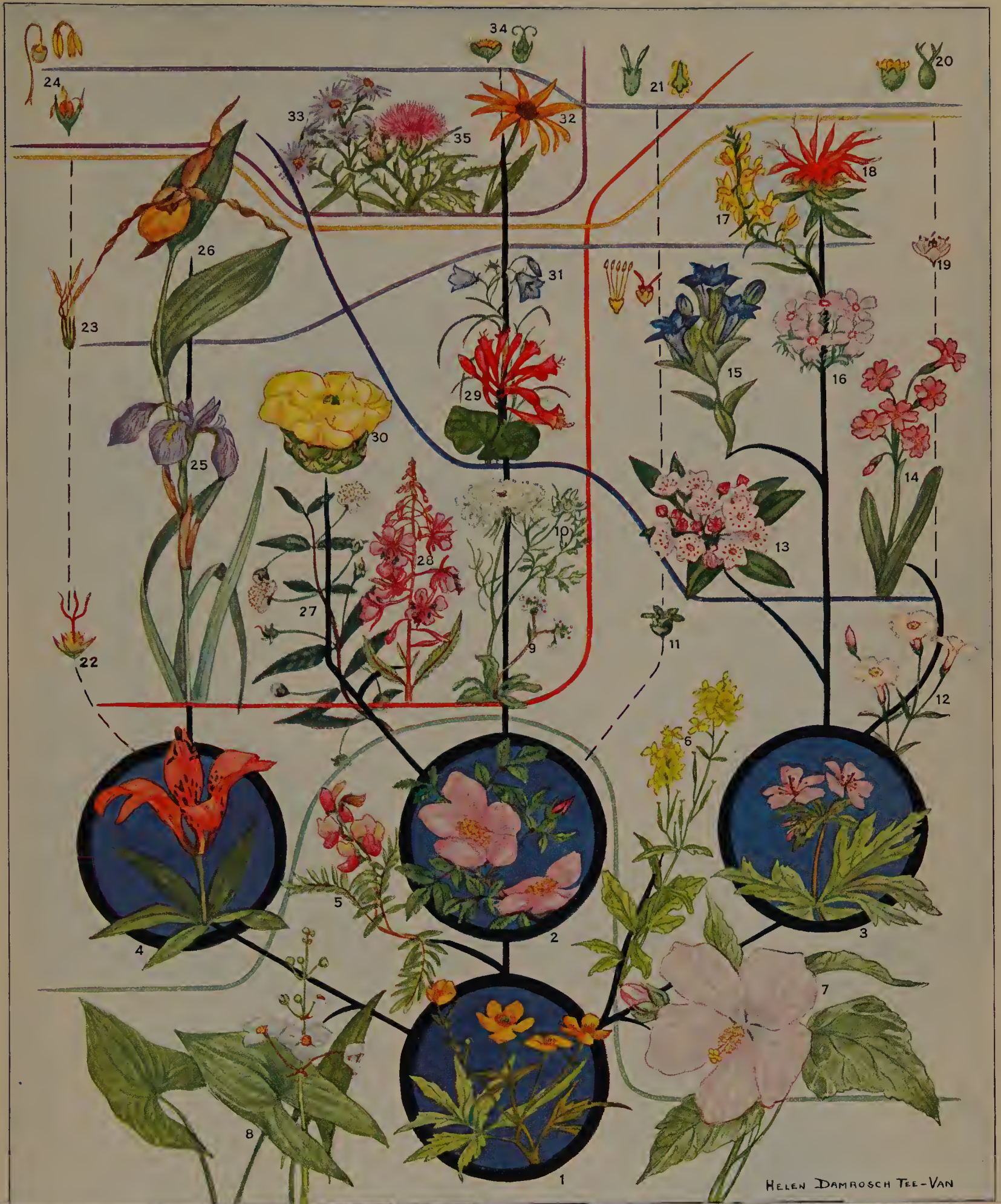
In compound indefinite inflorescences, the lateral shoots, developed centripetally, bear numerous bracteoles from which floral shoots arise, which may have a centripetal arrangement similar to that on the mother shoot, or a different one. Thus we may have a group of racemes arranged in a racemose manner; compound umbels as in most Umbelliferae (fig. 8); a raceme of capitula; a raceme of umbels, as in ivy, and so on.

The simplest type of definite inflorescence is where, as in *Anemone nemorosa*, the axis terminates in a single flower, no other flowers being produced on the plant. This is a *solitary terminal* inflorescence. When the primary floral axis, before ending in a flower, gives off lateral unifloral axes which repeat the process, the result is a *cyme*. A cyme with two axes is a *biparous* cyme or *dichasium* (fig. 11); with one axis, it is uniparous. In the dead-nettle (*Lamium*) the flowers arise in the axis of each foliage leaf and appear as if arranged in a whorl, but there is a central flower expanding first, and from its axis spring secondary axes bearing single flowers (fig. 10). The inflorescence is thus a dichasium and the clusters are called *verticillasters*. Where numerous lateral axes arise from the primary axis, a *cymose umbel* is produced. When these lateral axes grow strongly and develop irregularly, as in species of *Juncus*, the inflorescence is an *anthela*. In a uniparous cyme, the basal portion of the consecutive axes may become thickened and arranged more or less in a straight line, forming a false axis or *sympodium*, the inflorescence thus simulating a raceme. The uniparous cyme presents two forms; in a *scorpioid* cyme the flowers are arranged alternately in a double row along one side of the sympodium, the bracts forming another double row on the opposite side (*e.g.*, Boraginaceae). In a *helicoid* cyme, the flowers are in a single row and form a spiral round the false axis.

Compound definite inflorescences are by no means common, but in *Streptocarpus polyanthus* and in several calceolarias we probably have examples. Here we find *scorpioid cymes of pairs of flowers*, each pair consisting of an older and a younger flower.

Both the definite and indefinite types are represented in mixed inflorescences. Thus in the ragwort (fig. 12) the *heads* of flowers are developed centrifugally, while the *florets* open centripetally. Various combinations occur in different families.





## FLOWER DEVELOPMENT

This chart is founded on three basic features: (A) a starting point of primitive flower structure in the buttercups (1); (B) three great centre-roses (2), geraniums (3), and lilies (4)—each derived from the buttercup type, and (C) two main lines of development from each of these three centres. These main lines of development have resulted from the action of two great natural forces at work on the flower, namely, insects and wind. From each of the three chief centres broken dark lines indicate the course of development of

wind-pollinated flowers, while heavy dark lines show that of insect-pollinated flowers. In the lily line, for example, flower development as influenced by insects culminates in the orchids, while development influenced by the wind reaches its climax in the grasses. The most important changes in floral evolution are shown by coloured cross-lines: the first four from the bottom are concerned with insect-pollinated flowers; the upper three include wind-pollinated flowers as well

1. Buttercup. 2. Rose. 3. Geranium. 4. Lily.  
5. Wild Sweet Pea. 6. Mustard. 7. Rose Mallow.  
8. Arrow-head. 9. Saxifrage. 10. Carrot. 11.  
Sumach. 12. Pink. 13. Mountain Laurel. 14.

Primrose. 15. Gentian. 16. Phlox. 17. Toadflax.  
18. Oswego Tea. 19. Buckwheat. 20. Goosefoot.  
21. Walnut. 22. Rush. 23. Sedge. 24. Maize.

25. Iris. 26. Lady's-slipper. 27. Myrtle. 28.  
Willow-herb. 29. Honeysuckle. 30. Cactus. 31.  
Harebell. 32. Black-eyed Susan. 33. Aster. 34.  
Ragweed (*Ambrosia* sp.). 35. Thistle

FROM "FLOWER FAMILIES AND ANCESTORS" BY COURTESY OF F. E. AND E. S. CLEMENTS. PAINTED FOR THE ENCYCLOPÆDIA BRITANNICA BY HELEN DAMROSCH TEE-VAN









1. Inflorescence of the Lime; 2. Raceme of *Linaria striata*; 3. Head of *Scabiosa atropurpurea*; 4. Corymb of *Cerasus Mahaleb*; 5. Spike of *Vervain*; 6. Amentum of *Hazel*; 7. Spadix of *Arum maculatum* (female flowers below, male above); 8. Compound umbel of *Common Dill*; 9. Cymose inflorescence of *Cerastium colinum*; 10. Flowering *White Dead-Nettle*; 11. Scirpioid of *Forget-me-not*; 12. Flowering *Ragwort*; 13. Flower of *Sedum rubens*; 14. Completely symmetrical flower; 15. Flower of *Goosefoot*; 16. Stamen showing opening and shedding pollen; 17. Pistil of *Tobacco*; 18, 19 & 20. Diagrams illustrating hypogyny, perigyny, and epigyny of the flower; 21. Stamens of *White Water Lily*; 22. Flower of *Stonecrop*; 23. Flower of *Flax*; 24. Flower of *Heath*; 25. Flower of *Iris*; 26. Flower of *Fritillary*; 27. Flower of *Saxifrage*; 28 & 29. *Garden Pea*; 30. Reduplicate aestivation; 31. Contorted aestivation; 32. Quincuncial aestivation



*Tabular View of Inflorescences*

A. Indefinite Centripetal Inflorescences.

- I. Flowers solitary, axillary, *Veronica hederifolia*.
- II. Flowers in groups, pedicellate.
  - i. Elongated form (Raceme), *Hyacinth*; (Corymb), *Prunus*.
  - ii. Contracted form (Umbel), *Cowslip*.
- III. Flowers in groups, sessile.
  - i. Elongated form (Spike), *Plantago*.  
(Spikelet), *grasses*.  
(Catkin), *Hazel*.  
(Spadix), *Arum*.  
(Strobilus), *Hop*.
  - ii. Contracted form (Capitulum), *Daisy*.
- IV. Compound Indefinite Inflorescences.
  - a. Compound Spike, *Rye-grass*.
  - b. Compound Spadix, *Palms*.
  - c. Compound Raceme, *Astilbe*.
  - d. Compound Umbel, most *Umbelliferae*.
  - e. Raceme of Capitula, *Petasites*.
  - f. Raceme of Umbels, *Ivy*.

B. Definite Centrifugal Inflorescences.

- I. Flowers solitary, terminal, *Tulip*.
- II. Flowers in cymes.
  1. Uniparous Cyme.
    - a. Helicoid Cyme.
      - (i) Elongated, *Alstroemeria*.
      - (ii) Contracted, *Wittsteinia corymbosa*.
    - b. Scorpioid Cyme.
      - (i) Elongated, *Forget-me-not*.
      - (ii) Contracted, *Erodium*.
  2. Biparous Cyme (including Dichasium, Cymose Umbel).
    - a. Elongated, *Cerastium*.
    - b. Contracted (Verticillaster), *Dead-nettle*.
  3. Compound definite Inflorescence. Many *Calceolarias*.

C. Mixed Inflorescences.

- Raceme of Scorpioid Cymes, *Horse-chestnut*.  
 Scorpioid Cyme of Capitula, *Vernonia scorpioides*.  
 Compound Umbel of dichotomous Cymes, *Viburnum*.  
 Capitulum of contracted Scorpioid Cymes (Glomerulus), *Sea-pink*.  
 Cyme of Capitula, *Ragwort*.

**Parts of the Flower.**—The flower consists of the floral axis bearing the sporophylls (stamens and carpels) usually with protective envelopes. The axis is normally contracted, no internodes being developed and the portion bearing the floral leaves, the receptacle, is frequently a conical, flattened or hollowed expansion; rarely the axis is elongated and internodes are developed. Upon the receptacle the parts of the flower are crowded, usually forming a series of whorls, the parts of which alternate, but sometimes arranged spirally, especially if the axis is elongated. In a typical flower (fig. 22) there are four distinct whorls, an outer *calyx* of *sepals*; within it, the parts alternating with those of the calyx, is the *corolla* of *petals*; next alternating with the parts of the corolla, the *androecium* of *stamens*; and in the centre, the *gynoecium* of *carpels*. Fig. 14 is a diagrammatic representation (*floral diagram*) of such a flower, supposed to be cut transversely, the parts of each whorl being distinguished by a different symbol. The sepals are usually greenish, their function is mainly protective, shielding the delicate internal organs before the flower opens. The petals are usually showy. Sometimes (usually in monocotyledons) the calyx and corolla are similar; in such cases the term *perianth* is applied, and the parts of the calyx are *petaloid*. In some cases the petals resemble sepals (*sepaloid*). In plants, as *Nymphaea alba* (fig. 21), where a spiral arrangement of floral leaves occurs, these whorls pass insensibly into each other. When both calyx and corolla are present, the plant is *dichlamydeous*; when one is absent, *monochlamydeous* (fig. 15). Sometimes both are absent (*achlamydeous*), as in willow. The stamens in their most differentiated form, consist each of a stalk, the *filament* (fig. 16) consisting of *pollen-sacs* containing the powdery *pollen* (microspores) which is ultimately discharged. The *gynoecium* or *pistil* terminates the floral axis. It consists of one or more carpels (megaspores), separate or combined (fig. 17). The pistil is composed of the *ovary* (fig. 20), the lower portion enclosing the *ovules* destined to become seeds; and the *stigma* loose cellular

tissue, the receptive surface on which the pollen is deposited and either sessile on the apex of the ovary (poppy) or separated by a prolonged *style*. The androecium and gynoecium are not present in all flowers. When both are present the flower is *hermaphrodite* and is represented by the symbol ♂. When only one is present the flower is *unisexual* or *diclinous*, and is either male (*staminate*), ♂, or female (*pistillate*), ♀. When all four whorls of leaves are present the flower is *complete*. Usually the successive whorls of the flower, disposed from below upwards or from without inwards upon the floral axis, are of the same number of parts, or are a multiple of the same number of parts, those of one whorl alternating with those of the whorl next to it.

In the more primitive types of flower the receptacle is more or less convex, and the series of organs follow in regular succession, culminating in the carpels (fig. 18). This arrangement is *hypogynous*, the other series being beneath (*hypo*) the gynoecium. In other cases, the apex of the growing point ceases to develop and the parts below form a cup around it, from the rim of which the outer members of the flower are developed (perigynous, fig. 19). In many cases this is carried further and a cavity is formed roofed over by the carpels, so that the outer members of the flower spring from the edge of the receptacle which is immediately above the ovary (epigynous, fig. 20).

**Symmetry of the Flower.**—When a flower consists of parts arranged in whorls it is *cyclic*, and if all the whorls have an equal number of parts and are alternate it is *eucyclic* (figs. 14, 25). In contrast to cyclic flowers are those where the parts are in spirals (*acyclic*). Flowers which are cyclic at one portion and spiral at another (as many *Ranunculaceae*) are *hemicyclic*. In spiral flowers there is usually a gradual passage from sepaloid through petaloid to staminal parts (water lily, fig. 21). In some cases the parts of one whorl are opposite or *superposed* to those of the next. The superposition of the stamens on the sepals in the *Caryophyllaceae* is due to the suppression of the petals.

A flower is *symmetrical* when each whorl consists of an equal number of parts, or when the parts of any one whorl are multiples of that preceding it. Thus, a symmetrical flower may have five sepals, five petals, five stamens and five carpels (fig. 14) or the number of any of these parts may be a multiple of five. In the staminal whorl especially it is common to find additional rows. In fig. 24 the parts are in fours; in figs. 25 and 26, in threes. The floral envelopes are rarely multiplied. Flowers in which the number of parts in each whorl is the same are *isomerous*; when the number in some whorls is different, the flower is *anisomerous*. It often happens that when fully formed, the number of parts in the pistillate whorl is not in conformity with that in the other whorls. In such circumstances a flower is called symmetrical, provided that the other whorls are normal (fig. 27). A flower in which the parts are arranged in twos is *dimerous*; in threes, fours or fives, *trimerous*, *tetramerous* or *pentamerous* respectively. Trimerous symmetry is the rule in the monocotyledons, pentamerous the commonest in the dicotyledons, though dimerous and tetramerous flowers also occur in the latter group.

The various parts of the flower have a definite relation to the central axis. Thus in a tetramerous flower, one sepal may be next the axis (superior or posterior), another next the bract (inferior or anterior) and the other two *lateral* (fig. 24). A plane passing through the anterior and posterior sepals and through the floral axis is the *median* plane of the flower; a plane cutting it at right angles and passing through the lateral sepals, is the *lateral* plane; whilst the planes which bisect the angles formed by the lateral and median planes are *diagonal* planes. In a pentamerous flower one sepal may be superior (*Rosaceae* and *Labiatae*) or inferior (pea family, figs. 28, 29); in the latter case the odd petal (*vexillum*) is then superior. In the *Scrophulariaceae* one of the two carpels is posterior, the other anterior, whilst in the *Convolvulaceae* the carpels are lateral.

When the different members of each whorl are alike, the flower is *regular*; differences in size and shape of the parts of a whorl make the flower *irregular* (fig. 28). When a flower can be divided by a single plane into two similar parts it is *zygomorphic* (as in *Papilionaceae*). Polysymmetrical flowers have a radial sym-





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### BRITISH WILD FLOWERS

This group contains many of the most widely known and best beloved flowers of British waysides, fields and woods, all woven into the life and literature of the nation. Shakespeare, for example, sang of the oxlip and honeysuckle; Keats, of the poppy and foxglove; Shelley, of

the anemone; Campbell, of the hyacinth; Coleridge, of the wild rose; Heber, of the Scotch bluebell; Burns, of the daisy and hawthorn; Hogg, of the purple heather; and Alfred, Lord Tennyson, of the forget-me-not

1. Honeysuckle (*Lonicera Periclymenum*). 2. Foxglove (*Digitalis purpurea*). 3. Hawthorn (*Crataegus Oxyacantha*). 4. Harebell, Bluebell of Scotland (*Campanula rotundifolia*). 5.

Bluebell, Wild Hyacinth (*Scilla festalis*). 6. Oxlip, a species similar to the Cowslip. 7. Heather (*Erica cinerea*). 8. Red or Field Poppy

(*Papaver Rhoeas*). 9. Forget-me-not (*Myosotis scorpioides*). 10. English Daisy (*Bellis Perennans*). 11. Wild Rose (*Rosa canina*). 12. Wood Anemone (*Anemone nemorosa*)







metry and can be divided by several planes into similar portions; such are all regular, symmetrical flowers. When the parts of any whorl are not equal to, or some multiple of, the others, the flower is *asymmetrical*. This alteration in the symmetrical arrangement has been traced to *suppression* or *non-development* of parts, *degeneration* or imperfect formation, *cohesion* or union of parts of the same whorl, *adhesion* or union of parts of different whorls, *multiplication* of parts and *deduplication* (*chlorosis*) or splitting of parts. Cultivation has a great effect in causing changes in the various parts of a plant. The changes in colour and form of flowers thus produced are endless.

As a convenient method of expressing the arrangement of the parts of a flower, *floral formulae* have been derived. The following is a simple mode: the whorls are represented by the letters *S* (sepals), *P* (petals), *A* (stamens), *C* (carpels) and a figure marked after each indicates the number of parts in that whorl. Thus *S5P5A5C5* means that the flower is perfect, isomerous and pentamerous. The flower of *Sedum* (fig. 22) would be represented by *S5P5A5+5C5*, where *A5+5* indicates that the staminal whorl consists of two rows of five parts each.

**Aestivation.**—The manner in which the parts are arranged in the flower-bud with respect to each other before opening is the *aestivation* or *præfloration*, and distinctive names have been given to the different arrangements exhibited, both by the leaves individually and in their relation to each other. As regards each leaf of the flower, it is either spread out, as the sepals in the bud of the lime-tree, or folded upon itself (conduplicate), or slightly folded inwards or outwards at the edges, as in the calyx of some species of *Clematis*, or rolled up at the edges (involute or revolute), or folded transversely, becoming *crumpled* or *corrugated* as in the poppy.

When the parts of a whorl are in an exact circle, and are applied to each other by the edges only, without overlapping or folding, aestivation is *valvate*. The edges of each of the parts may be turned inwards (induplicate) or outwards (reduplicate). When the parts of a single whorl are placed in a circle, each of them exhibiting torsion so that by one of its sides it overlaps its neighbour, whilst its side is overlapped in like manner by that standing next to it, aestivation is *twisted* or *contorted*. When the flower expands, traces of twisting sometimes remain. These forms of aestivation occur in cyclic flowers and are included under *circular* aestivation. In spiral flowers the leaves may cover each other partially, like tiles on a house, or the parts may envelop each other completely (*convolute*). When the parts are five, as in many dicotyledons, there may be two parts external, two internal and a fifth which partially covers one of the inner parts by its margin and is in turn partially covered by one of the external parts (*quincuncial*), as in the corolla of Rosaceae. In the Leguminosae, the vexillum is often large and folded over the others (*vexillary*) or the carina may perform a similar office (*carinal*). Circular aestivation is generally associated with a regular calyx and corolla while spiral aestivation is connected with irregular as well as regular forms.

### FLORAL ENVELOPES

**Calyx.**—The sepals are sometimes *free* or separate from each other, at other times united to a greater or less extent; in the former case, the calyx is *polysepalous*, in the latter *gamosepalous* or *monosepalous*. The divisions of the calyx are usually entire, but occasionally are cut (rose); rarely they are stalked. Sepals are generally more or less oval, elliptical or oblong, with blunt or acute apices. They may be erect or reflexed, spreading downwards (*divergent* or *patulous*) or arched inwards (*connivent*). They are usually greenish (*herbaceous*) but sometimes they are coloured (*petaloid*). The vascular bundles sometimes form a prominent mid-rib, at other times, several ribs. The venation is useful as pointing out the number of leaves in a gamosepalous calyx. A polysepalous calyx with three sepals is *trisepalous*, with five, *pentasepalous*, etc. The sepals are occasionally of different forms and sizes. The number of members in a gamosepalous calyx is usually marked by divisions at the apex, which may be simple projections or may extend down as fissures, the calyx

being *trifid* (three-cleft), *quinquefid* (five-cleft), etc.; or they may reach nearly to the base, the calyx being *tripartite*, *quinquepartite*, etc. The union of the parts may be complete and the calyx entire or *truncate*. The cohesion is sometimes irregular; thus a two-lipped or *labiate* calyx arises. Occasionally certain parts of the sepals are enlarged to form a spur as in *Tropaeolum*, *Viola* and *Pelargonium*. Degeneration may take place so that the calyx becomes dry and scaly (Juncaceae); or hairy (Compositae); or a mere rim (madder), when it is *obsolete* or *marginate*. In Compositae, the calyx is attached to the pistil and its limb is developed into hairs (*pappus*). The calyx sometimes falls off before the flower opens, as in poppies (*caducous*, fig. 36); or with the corolla, as in *Ranunculus* (*deciduous*), or it remains after flowering (*persistent*) as in Labiatae, or its base only is persistent (*operculate*). The receptacle bearing the calyx is sometimes united to the pistil and enlarges to form part of the fruit (apple), in which case the withered calyx is seen at the apex. Sometimes a persistent calyx encloses the fruit without being incorporated with it (*accrescent*); or it may become *inflated* or *vesicular* (*Lychnis*).

**Corolla.**—The corolla is the coloured attractive inner floral envelope; usually the most conspicuous whorl. As a rule the petals are highly coloured, the colouring matter being contained in the cell-sap (blue and red flowers) or in *plastids* (*chromoplasts*) as in yellow flowers, or in both (orange flowers). Petals are generally glabrous, but in some instances hairs are produced. They often close the way to the honey-secreting part of the flower to small insects whose visits would be useless for pollination. Coloured hairs occur on the perianth of *Iris*. Normally thin and delicate petals occasionally become thick and fleshy (*Rafflesia*), dry (heaths), or hard and stiff (*Xylopi*). Each petal often consists of two parts, a lower narrow *unguis* or *claw*, and an upper, broad *lamina* or *limb* (fig. 38). The claw is often wanting (fig. 39) and the petals are then *sessile*. The limb may be flat, concave or hollowed. In hellebore the petals become tubular (fig. 40); in aconite (fig. 42), some resemble a hollow-curved horn, supported on a grooved stalk; while in columbine and violet (fig. 41) one or all are prolonged as a spur. In *Antirrhinum*, the spur is short and the petal is *gibbous* or *saccate*. These spurs, tubes and sacs serve as receptacles for nectar.

A corolla is *dipetalous*, *tripetalous*, etc., according as it has two, three, etc., separate petals; the general name *polypetalous* is given to corollas with separate petals, while those in which the petals are united are *monopetalous*, *gamopetalous* or *sympetalous*. This union generally takes place at the base and extends towards the apex. In the vine, the petals are separate at the base, adherent at the apex. In a sympetalous corolla the lower portion usually forms a tube, the upper parts a common limb, the point of union being the *throat*. The number of parts is determined by the divisions (teeth, fissures, etc.), or when, as rarely, the corolla is entire, by the venation. The union may be equal, or some parts may unite more than others.

Amongst regular polypetalous corollas may be noticed the *rosaceous* corolla; the *caryophyllaceous* corolla, in which there are five clawed petals; the *cruciform*, having four petals in the form of a cross, as in the wallflower. Of irregular polypetalous corollas, the most marked is the *papilionaceous* (fig. 28–29), in which there are five petals—one superior next to the axis, usually larger than the rest, and the *vexillum* or *standards*, two lateral, the *alae* or wings; two inferior, often united slightly to form a single keel or carina, which embraces the essential organs.

Regular sympetalous corollas may be *campanulate* or *bell-shaped* (*Campanula*); *hypocrateriform* or *salver-shaped* (*Primula*, fig. 43) *tubular* (comfrey); *rotate* or *wheel-shaped* (forget-me-not); *urceolate* or *urn-shaped* (bell-heath). Some of these forms may become irregular in consequence of certain parts being more developed than others; thus in the foxglove there is a slightly irregular campanulate corolla. Other irregular sympetalous corollas include the *labiate* or *lipped*, having two divisions of the limb, the upper usually of two, the lower of three, united petals, separated by a gap. When the upper lip is much arched, and the gap is distinct, the corolla is *ringent*; when the gap is reduced





33. Imbricated aestivation; 34. Vexillary aestivation; 35. Groundsel fruit with pappus; 36. Poppy calyx; 37. Fruit of *Physalis Alkekengi*; 38. Ungulculate petal of Wallflower; 39. Crowfoot petal; 40. Hellebore petal; 41. Pansy; 42. Part of Aconite flower; 43. Primrose flower; 44. Dandelion flower; 45. Stamens of Garden Pea; 46. Anther of Rush; 47. *Salvia officinalis* anther; 48. Nightshade stamen; 49. Barberry stamen; 50. Flower of Wallflower; 51. Pollinia; 52. *Asclepias* pistil; 53. Broom pistil; 54. Section of Black Hellebore flower; 55. Strawberry; 56. Section of Dog Rose fruit; 57. *Ranunculus* pistils; 58. Flax pistil; 59. Garden Pea fruit; 60. Ovary of Lily; 61. Quinquelocular ovary; 62. Five-carpellary ovary; 63. Melon fruit; 64. *Cerastium hirsutum* pistil; 65. Same cut horizontally; 66. Carpel of Lady's mantle; 67. Primrose pistil; 68. Grass flower with glumes removed; 69. *Polygonum Convolvulus* ovary; 70. Gynaecium and stamen of Poppy; 71. Ovules; 72. Ovules; 73. Ovule



to a chink, as in snapdragon, *personate*. In *Calceolaria* the lips become much hollowed out. When a tubular corolla is split to form a strap-like process on one side, it is *ligulate* or *strap shaped* (fig. 44), as in many Compositae.

Petals are sometimes suppressed and at times the whole corolla is absent. In *Amorpha* there is only a single petal. In the Ranunculaceae some genera (e.g., *Ranunculus*) have both calyx and corolla, while others (e.g., *Anemone*) have only a coloured calyx.

The term *nectary* includes those parts of a flower which secrete a honey-like substance, as the glandular depression on the petal of *Ranunculus* (fig. 39). The honey attracts insects, which convey pollen to the stigma. The horn-like nectaries under the galeate sepal of *Aconitum* (fig. 42) are modified petals, as are the tubular nectaries of hellebore (fig. 54).

Petals are attached to the axis usually by a narrow base. When this attachment is by an articulation, the petals fall off either immediately after expansion (*caducous*) or after fertilisation (*deciduous*). A corolla continuous with axis, as in *Campanula*, may remain in a withered state while the fruit is ripening. A sympetalous corolla falls off in one piece.

### ESSENTIAL ORGANS

As a stamen represents a leaf developed to bear pollen or microspores, it is spoken of in comparative morphology as a microsporophyll; similarly the carpels which make up the pistil are the megasporophylls (see ANGIOSPERMS). In plants with hermaphrodite flowers, self-fertilisation is often provided against by the structure of the parts or by the period of ripening of the organs. For instance, in *Primula* (fig. 43), some flowers (thrum-eyed) have long stamens and a short styled pistil, others (pin-eyed) short stamens and a long-styled pistil; these are *dimorphic*. In some plants the stamens are perfected before the pistil (*protandrous*); more rarely, the pistil is perfected first (*protogynous*). Plants in which protandry or protogyny occur are *dichogamous*. When the same plant bears unisexual flowers of both sexes it is *monoecious* (hazel); when the male and female flowers are on separate plants, the plant is *dioecious* (hemp); when there are male, female and hermaphrodite flowers, it is *polygamous*.

**Stamens.**—The stamens arise from the receptacle within the petals, with which they generally alternate, forming one or more whorls, collectively constituting the androecium. Their normal position is below the pistil (*inferior*), but they may be above (*superior*) or, as in Saxifragaceae, *half inferior* or *half superior*. Sometimes they adhere to the petals (*epitalous*), or to the pistil, so as to form a column (*gynandrous*). These arrangements are important in classification. Stamens vary in number from one to many, even hundreds. In acyclic flowers there is often a gradual transition from petals to stamens, as in the white water lily (fig. 21). When there is only one whorl the stamens are usually equal in number to the sepals or petals. The additional rows of stamens may be developed in centripetal order or interposed between the pre-existing ones or placed outside them, i.e., be developed centrifugally (geranium). When the stamens are fewer than 20, they are *definite*; when more, *indefinite*, represented by the symbol  $\infty$ . A flower with one stamen is *monandrous*, with two, *diandrous*, with many, *polyandrous*, etc.

The function of the stamen is the development and distribution of the pollen, which is contained in the anther. If the latter is absent, the stamen cannot perform its functions. The anther is developed before the filament, which may be absent (e.g., mistletoe), when the anther is *sessile*.

**The Filament.**—The filament is usually thread-like and cylindrical, or slightly tapering towards its summit. It may, however, be thickened and flattened in various ways. The length sometimes bears a relation to that of the pistil, and to the position of the flower. Though usually of sufficient solidarity to support the anther in an erect position, the filament is sometimes (e.g., grasses) delicate and hair-like, so that the anther is pendulous (fig. 68). It is generally continuous, but sometimes is bent or jointed (*geniculate*), or spiral (e.g., pellitory). In *Fuchsia* it is red, in *Adonia*, blue; in *Ranunculus acris*, yellow. The filament

is usually articulated to the receptacle and the stamen falls off after fertilisation, but in *Campanula*, the stamens remain in a withered state. The filaments may cohere to a greater or lesser extent, the anthers remaining free. Thus, all the filaments may unite to form a tube round the pistil (e.g., mallow), the stamens being *monadelphous*, or they may be arranged in two bundles (*diadelphous*), as in the pea, where nine out of ten unite, the posterior one being free (fig. 45). In this case the stamens, originally free, cohere, but in most cases each bundle arises from the branching of a single stamen.

**The Anther.**—The anther consists of lobes containing the minute pollen grains, which, when mature, are discharged by an opening. There is a double covering to the anther—the outer *exothecium* resembling the epidermis and often bearing stomata; the inner *endothecium* formed by a layer or layers of cellular tissue, the cells of which have thickened walls. The endothecium generally becomes thinner towards the part where the anther opens out, and there disappears. The anther appears first as a simple papilla of meristem, upon which indications of two lobes soon appear. Upon these projections rudiments of the pollen-sacs, usually four, two on each lobe, are seen. In each differentiation takes place in the layers beneath the epidermis, by which an outer small-celled layer surrounds an inner one of larger cells. These central cells are the pollen mother-cells, the outer cells forming the endothecium while the exothecium arises from the epidermis.

When all four pollen-sacs remain permanently the anther is *quadrilocular* (fig. 46). Sometimes, however, the sacs in each lobe unite to give a *bilocular* anther. Further fusion of the lobes or the abortion of one of them (e.g., hollyhock) leads to a *unilocular* anther. Occasionally there are numerous cavities in the anther (e.g., mistletoe). The lobes are generally more or less oval or elliptical. The division between them is marked on the face of the anther by a *furrow*, and there is usually a suture indicating the line of dehiscence. Stamens may cohere by their anthers becoming *syngenesious* (e.g., Compositae).

**The Connective.**—The anther-lobes are united by the *connective* which is either continuous with the filament or articulated with it. When the filament is continuous and prolonged so that the lobes appear to be united throughout their length, the anther is *adnate* or *adherent*. When the filament ends at the base of the anther, the latter is *innate* or *erect*. In these cases the anther is fixed. When, however, the attachment is narrow and an articulation exists, the anthers are movable (*versatile*) as in grasses (fig. 68). The connective is sometimes extended backwards and downwards (e.g., violet) to form a nectar-secreting spur.

**Anther Dehiscence.**—The opening or dehiscence of the anthers to discharge their content takes place by clefts, valves or pores. When the anther-lobes are erect, the cleft is likewise along the line of suture—*longitudinal dehiscence* (fig. 16). In other instances the opening is confined to the base or apex, each loculus opening by a single pore (e.g., *Solanum*, fig. 48); in the mistletoe there are numerous pores. In the barberry (fig. 49) each lobe opens by a valve on the outer side of the suture (*valvular*). Anthers dehisce at different periods during the process of flowering, sometimes in the bud but more commonly when the flower is expanded. They may dehisce simultaneously or in succession. These variations are connected with the arrangements for the transference of pollen. *Introrse* anthers dehisce by the surface next the centre of the flower, *extrorse* anthers by the outer surface; when by the sides (e.g., *Iris*) they are *laterally* dehiscent.

Stamens occasionally become sterile by non-development of the anthers and are then called *staminodes*. Some stamens are enclosed within the tube of the flower (*included*) others are *exserted*, i.e., extend beyond the flower (e.g., *Plantago*); sometimes they are exserted in early growth, but become included later (e.g., *Geranium striatum*). When there is more than one whorl, the stamens on the outside are often longest (e.g., many Rosaceae), but sometimes the reverse is the case. When the stamens are in two rows, those opposite the petals are usually the shorter. In some flowers the stamens are *didynamous*, only four out of five



being developed and the upper pair longer than the lateral (e.g., Labiatae, Scrophulariaceae). When there are six stamens, four may be long and two short (*tetradynamous*), alternating with the pairs of long ones (e.g., Cruciferae, fig. 50).

**Pollen.**—The pollen-grains consist of small cells, developed from the large, thick-walled mother-cells in the interior of the pollen-sacs. A division takes place to form four cells in each mother-cell and these are the pollen grains, which increase in size and acquire a cell-wall, differentiated into an outer cuticular *extine* and an inner *intine*. Then the walls of the mother-cells are absorbed and the grains float freely in the fluid of the pollen-sacs. The fluid gradually disappears and the mature grains form a powdery mass. In most Orchidaceae the pollen-grains are united into masses (pollinia, figs. 51, 52) by viscid matter. Each of these has a stalk (*caudicle*) which adheres to a prolongation at the base of the anther (*rostellum*) by a viscid gland (*retinaculum*). *Gynandrium* is sometimes applied to the part of the column in orchids where the stamens are situated. The number of pollinia varies.

The extine is a firm membrane which defines the contour of the pollen-grain and gives it colour (generally yellow). The extine is either smooth or covered with projections and is often covered with viscid or oily matter. The intine is uniform, thin, transparent and extensible. In some aquatics (e.g., *Zostera*) only one covering exists.

Pollen-grains vary in diameter from  $\frac{1}{300}$  to  $\frac{1}{700}$  in. or less. They are most commonly ellipsoidal, but may be spherical, cylindrical and curved, polyhedral (Compositae) or nearly triangular in section. There are rounded pores varying from one to fifty, and through one or more of these the pollen-tube is extruded in germination. In monocotyledons there is usually only one, in dicotyledons, where they may form a circle round the equatorial surface, they number from three upwards. Within the pollen-grain is granular protoplasm with oily particles and occasionally starch. Before leaving the pollen-sac, the grain divides into a vegetative cell or cells, from which the pollen-tube arises, and a generative cell, forming the male cells (see ANGIOSPERMS, GYM-NOSPERMS).

**Pollination.**—When the pollen-sacs are ripe, the anther dehisces and the pollen is shed. In order that fertilization may be effected, the pollen must be conveyed to the stigma of the pistil. This *pollination* (q.v.) is promoted in various ways, the whole form and structure of the flower being adapted to the process. In some plants (e.g., pellitory) the mere elasticity of the filament is sufficient; in others (*anemophilous*) pollination is effected by the wind (e.g., grasses) and in such cases enormous quantities of pollen are produced; but the common agents of pollination are insects. To attract them to the flower the odoriferous secretions and gay colours are produced, and the position and complicated structure of the parts of the flower are adapted to the perfect performance of the process. It is comparatively rare in hermaphrodite flowers for self-fertilization to occur and the various forms of dichogamy, dimorphism and trimorphism prevent this.

**Disk.**—Under the term disk is included every structure intervening between the stamens and the pistil. It presents great varieties of form, such as a ring, scales, glands, hairs, petaloid appendages, etc., and often contains nectar. The disk frequently arises by degeneration or transformation of the staminal row. In cruciferae, it consists of tooth-like scales at the base of the stamens. The enlarged receptacle covering the ovary in *Nymphaea* may be regarded as a disk.

**The Pistil.**—The pistil or gynoecium occupies the centre or apex of the flower and is surrounded by the stamens and floral envelopes when these are present. It constitutes the innermost whorl, which after flowering is changed into the fruit and contains the seeds. The ovary contains the ovules attached to the *placenta*. The pistil consists of one or more modified leaves, the *carpels* (megasporophylls). When a pistil consists of a single carpel, it is *simple* or *monocarpellary* (fig. 53); when composed of several carpels, it is *compound* or *polycarpellary* (fig. 54). Each carpel has its own ovary, style (when present) and stigma and may be regarded as formed by a folded leaf, the upper

surface of which is turned inwards, towards the axis; the lower outwards, while the ovules develop from the margins. A pistil is usually formed by more than one carpel. These may be arranged at the same height in a whorl, or at different heights in a spiral. When they remain separate and distinct (e.g., hellebore, fig. 54) the pistil is *apocarpous*; when they unite (e.g., pear) it is *syncarpous*. A flower with a simple pistil is *monogynous*; with two carpels, *digynous*, with three, *trigynous*, etc.

The union in a syncarpous pistil is not always complete; it may take place by the ovaries alone (fig. 58), when the organ becomes a compound ovary; or by ovaries and styles; or by stigmas and the summits of these styles. Various intermediate states exist; the union is usually most complete at the base.

**The Placenta.**—The ovules are attached to the placenta, through which the fibrovascular bundles pass. The placenta is usually formed on the edges of the carpellary leaf (*marginal placentation*). But often the placentas arise from the axis (*axile placentation*) and are not connected with the carpellary leaves. In marginal placentation, the placenta is borne on the *inner* or *ventral suture*, corresponding to the margin of the carpellary leaf, the *outer* or *dorsal suture* corresponding to the mid-rib. As the placenta is formed on each margin of the carpel, it is essentially double. When the pistil is simple, the inner margins unite and usually form a common placenta. When the pistil is apocarpous, there are generally separate placentas at each margin. In a syncarpous pistil, however, the carpels are so united that the edges of each of the contiguous ones, by their union, form a *septum* or *dissepiment*, and the number of these septa consequently indicates the number of carpels in the pistil. When the septa extend to the axis, the ovary is divided into cells, being *bilocular*, *trilocular*, etc., according to the number, each cell corresponding to a single carpel. In these cases, the marginal placentas meet in the axis and unite to form a single *central* one. When the carpels of a syncarpous pistil do not fold inwards, the ovary is *unilocular* and the placentas are *parietal* (e.g., *Viola*). Often the margins of the carpels which fold in to the centre split there into two lamellae, each of which is curved outwards and projects into the loculament, dilating at the end into a placenta (e.g., Cucurbitaceae, fig. 63). Cases occur, however, in which the placentas are not connected with the walls of the ovary (*free central placentation*, figs. 64, 65); this may be due to the separation of the carpellary leaves from the axis, as in Caryophyllaceae, in which there are often traces of the septa at the base of the ovary; or to the placenta being an axile formation produced by the elongation of the axis (e.g., Primulaceae).

Occasionally divisions take place in ovaries which are not formed by the edges of contiguous carpels. These *spurious dissepiments* are often horizontal, only developed after fertilization. In Cruciferae, however, they are vertical and arise from the prolongation of the placentas.

The ovary is usually spherical or curved, sometimes smooth on its surface, at other times hairy and grooved. The grooves usually indicate the divisions between the carpels. When the ovary is on the centre of the receptacle, free from the outer whorls, so that its base is above the insertion of the stamens, it is *superior* (e.g., *Primula*, figs. 43, 67). When the margin of the receptacle is prolonged upwards, carrying with it the floral envelopes and staminal leaves, the basal portion of the ovary being formed by the receptacle and the carpellary leaves alone closing the apex, the ovary is *inferior* (e.g., *Fuchsia*). In many Saxifragaceae these are intermediate forms (*half-inferior*).

**The Style.**—The style proceeds from the summit of the carpel (fig. 67) and is traversed by a narrow canal, a continuation of the placenta, constituting conducting tissue, which ends in the stigma. In some cases, owing to more rapid growth of the dorsal side of the ovary, the style becomes lateral (fig. 66); this may be accentuated so that the style appears to arise from the base (*basilar*); but it still indicates the organic though not the apparent, apex of the ovary. Several basilar styles may unite (e.g., Boraginaceae) to form a single *gynobasic* style. The style is usually cylindrical, filiform and simple; sometimes it is grooved on one side, or flat, thick, angular, compressed or even petaloid





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### NORTH AMERICAN WILD FLOWERS

Some 12,000 kinds of flowering plants grow wild in the United States and Canada, many of which are noted for their handsome flowers. Conspicuous groups are the asters, golden rods, lilies, phloxes, columbines and gentians, found across the continent; mag-

nolias and azaleas especially in the South; trilliums and violets in the East; and lupines and poppies in the West. See articles on the different flowers. (St. fl. is placed after such flowers as have been adopted as State flowers.)

1. Orange Lily (*Lilium canadense*). 2. Summer Phlox (*Phlox paniculata*). 3. Golden Rod (*Solidago canadensis*), St. fl., Ala., Nebr. 4. Bluebonnet (*Lupinus texensis*), St. fl., Texas. 5. Cardinal Flower (*Lobelia cardinalis*). 6.

Blue Columbine (*Aquilegia caerulea*), St. fl., Colo. 7. New England Aster (*Aster novae-angliae*). 8. Moccasin Flower (*Cypripedium acaule*), St. fl., Minn. 9. California poppy

(*Eschscholtzia californica*), St. fl., Calif. 10. Fringed Gentian (*Gentiana crinita*). 11. Magnolia (*Magnolia grandiflora*), St. fl., La. and Miss. 12. Trailing Arbutus (*Epigaea repens*), St. fl., Mass.







(e.g. *Iris*). It may bear hairs, which aid in the application of pollen to the stigma (collecting hairs, e.g. *Campanula*). The styles of a syncarpous pistil, when separate, alternate with the septa; when united, the style is *simple* (fig. 67). The style of a single carpel may be divided. The length of the style depends upon the relation which should subsist between the position of the stigma and that of the anthers to allow proper application of pollen.

**The Stigma.**—The stigma is the termination of the conducting tissue of the style and is usually in direct communication with the placenta. It consists of loose cellular tissue and secretes a viscid matter which detains the pollen and causes it to germinate. The stigmas alternate with the septa of a syncarpous pistil, *i.e.* corresponds to the back of the loculi; but in some cases half the stigma of one carpel unites with half that of the next, the stigmas being thus opposite the septa (e.g. poppy). The divisions of the stigma usually mark the number of carpels in the pistil, but sometimes (e.g. Gramineae) the stigma of a single carpel divides. It may be terminal or lateral and may present sensitive laminae which close when touched (e.g. *Mimulus*). It may be globular, umbrella-like, ovoid (e.g. *Fuchsia*), radiating, as in the poppy, where the true stigmatic rays are attached to a shield-like (*pel-tate*) body. The lobes of the stigma may be flat and pointed, fleshy and blunt, smooth, granular or feathery (e.g. many grasses, fig. 68). In Orchidaceae, the stigma is on the anterior surface of the column beneath the anthers.

**The Ovule.**—The ovule is usually produced on the margin of the carpellary leaf, but sometimes ovules arise all over the surface of the leaf, or from the floral axis, terminally (e.g. Polygonaceae) or laterally (e.g. Primulaceae). The ovule is usually contained in an ovary and is *angiospermous*; but in the Coniferae and Cycadaceae it has no proper ovarian covering and is *naked* or *gymnospermous*. It is attached to the placenta either directly (*sessile*) or by a *funicle* (figs. 71, 72, 73); this cord may become much elongated after fertilization. The ovule is attached to the placenta or funicle by its *base* or *hilum*, the opposite end being its *apex*.

The ovule first appears as a small projection from the placenta. The cells multiply and assume an enlarged ovate form constituting the *nucellus*. This nucellus may remain naked and alone form the ovule, as in some parasitic families; but in most plants it becomes surrounded by integuments, which appear first as rings at the base of the nucellus, which gradually spread over its surface. In some cases (e.g., Compositae), only one covering is formed, but usually another is developed subsequently, covering the first completely except at the apex, where neither integument invests the nucellus, but leaves an opening, the *micropyle*. A single cell of the nucellus enlarges to form the *embryo-sac* or *megaspore*, which gradually supplants the tissue of the nucellus until only a thin layer is left, and at the apex it may extend beyond it, or pass into the micropyle. In gymnosperms it usually remains deep in the nucellus. For further development, see ANGIOSPERMS, GYM-NOSPERMS.

The point where the integuments are united to the base of the nucellus is the *chalaza*, which is often coloured, is denser than the surrounding tissue and is traversed by vascular bundles from the placenta. When the chalaza is at the hilum and the micropyle is opposite, there being a short funicle, the ovum is *orthotropous* (fig. 72). When by more rapid growth on one side than on the other, the nucellus and integuments are curved on themselves so that the micropyle approaches the hilum, the ovule is *campylotropous* (e.g., Cruciferae, fig. 71). In an *inverted* or *anatropous* ovule (fig. 73) the commonest form in angiosperms, the apex with the micropyle is turned towards the point of attachment of the funicle to the placenta and the funicle coalesces with the ovule to form the *raphe*. The ovule thus curves from the point of origin of the integuments and if a second integument is formed, it does not extend to the side adherent to the raphe. Forms intermediate between these types occur. When there is a single ovule with its axis vertical, it may be attached to the placenta at the base of the ovary (*basal placenta*), when it is erect (e.g., Compositae); or it may be inserted a little above the base on a parietal placenta

(ascending); or it may hang from an apical placenta at the summit of the ovary, its apex being directed downwards (*inverted* or *pendulous*); or from a parietal placenta near the summit (*suspended*, e.g., Euphorbiaceae). Sometimes a long funicle arises from a basal placenta, reaches the summit of the ovary and there, bending over, suspends the ovule (e.g., sea-pink); at other times the hilum appears to be in the middle and the ovule is *horizontal*. When there are two ovules in the same cell they may be side by side (*collateral*); or one erect and the other inverted; or one above the other, as is the case in ovaries containing a moderate number of ovules. When the ovules are *definite* (*i.e.*, uniform and can be counted) their attachment usually forms a good character for classification. When very numerous (indefinite) and the placenta little developed, their position shows great variation and their form is altered by pressure into various polyhedral shapes.

**Fertilization.**—When the pistil has reached a certain stage in growth, it becomes ready for fertilization. The pollen-grain having reached the stigma in angiosperms, or the summit of the nucellus in gymnosperms, it is detained there, and the viscid secretion from the glands of the stigma or from the nucellus induce the protrusion of a pollen-tube through the pores of the grain. The pollen-tube (or tubes) passes down the canal (fig. 69), through the conducting tissue of the style, when present, and thence to the micropyle of the ovule, one pollen-tube going to each ovule. Frequently the tube has to pass some distance into the ovary, to reach the micropyle, being guided by hairs, grooves, etc. In gymnosperms the pollen-grain resting on the apex of the nucellus sends off its pollen-tubes which at once penetrate the nucellus (fig. 69). Ultimately the apex of the tube perforates the tip of the embryo-sac, the male cells are transmitted to the sac and fertilization is effected. Consequent upon this, after a longer or shorter period, those changes begin in the embryo-sac which result in the formation of the embryo plant, the ovule being converted into the seed, the ovary enlarging to form the fruit, often incorporated with which are other parts of the flower (receptacle, calyx, etc.). In gymnosperms the pollen-tubes, having penetrated a certain distance down the tissue of the nucellus, are arrested in growth for a period, sometimes nearly a year. See ANGIOSPERMS: Flower; FRUIT; SEED.

**LATEX**, a fluid found in the cells of angiospermous plants, consisting of an emulsion of various substances suspended in a watery medium in which salts, sugars, tannins, alkaloids, enzymes and other substances are dissolved. This lactiferous fluid circulates in branched tubes which penetrate the tissues of the plant in a longitudinal direction. It has an important function in conducting plastic substances in addition to acting as an excretory reservoir. The Para rubber tree (*Hevea brasiliensis*) is regularly tapped, the coagulated latex which it exudes being worked up into rubber. Opium is obtained from the latex of the opium poppy (*Papaver somniferum*) which contains the alkaloid morphine. See PLANTS and FUNGI.

**NUT**, a term applied to that class of fruit which consists generally of a single kernel enclosed in a hard shell. Botanically speaking, nuts are one-celled fruits with hardened pericarps, sometimes enveloped in a cupule or cup, formed by the aggregation of the bracts as in the hazel and the acorn. A great number of nuts enter into commerce for various purposes, principally as articles of food or sources of oil, and for several ornamental and useful purposes. The edible nuts are very rich in oil, with a small percentage of the other carbohydrates, starch, sugar, etc., and also a large proportion of nitrogenous constituents. Oleaginous nuts used for food are likewise employed more or less as sources of oil, but on the other hand there are many oil-nuts of commercial importance not embraced in the list of edible nuts.

On the following page is set out an alphabetical enumeration of the more important nuts, and of products passing under that name, used either as articles of food or as sources of oil.

There remain to be enumerated a number of nuts of commercial value for turnery and ornamental purposes, for medicinal use, and for several miscellaneous applications in the arts. See table.

The application of the term nut to many of these products is purely arbitrary, and it is obvious that numerous other bodies



Name	Source	Locality	Remarks
Almond . . . . .	<i>Prunus Amygdalus</i> , var. <i>dulcis</i> . . . . .	S. Europe . . . . .	Food, oil.
Almond (bitter) . . . . .	<i>Prunus Amygdalus</i> , var. <i>amara</i> . . . . .	.. . . .	Oil.
Ar nut or earth nut . . . . .	Tubers of <i>Bunium flexuosum</i> and other species . . . . .	W. Europe (Britain) . . . . .	Food.
Bambarra ground nut . . . . .	<i>Voandzeia subterranea</i> . . . . .	Tropics, especially Africa . . . . .	Food.
Ben nut . . . . .	<i>Moringa oleifera</i> (a winged seed) . . . . .	India . . . . .	Oil.
Bitter nut . . . . .	<i>Carya cordiformis</i> (swamp hickory) . . . . .	N. America . . . . .	See HICKORY.
Brazil nut . . . . .	<i>Bertholletia excelsa</i> . . . . .	S. America . . . . .	Food, oil.
Bread nut . . . . .	<i>Brosimum Alicastrum</i> . . . . .	W. Indies . . . . .	Food.
Butter or Souari nut . . . . .	<i>Caryocar nuciferum</i> . . . . .	Guiana . . . . .	Food.
Cahoun nut . . . . .	<i>Attalea Cohune</i> . . . . .	Honduras . . . . .	Oil.
Candle nut . . . . .	<i>Aleurites triloba</i> . . . . .	S. Sea Islands . . . . .	Oil.
Cashew nut . . . . .	<i>Anacardium occidentale</i> . . . . .	W. Indies and Tropical America . . . . .	Food, oil.
Chestnut . . . . .	<i>Castanea vesca</i> . . . . .	S. Europe . . . . .	Food.
Cob, filbert, or hazel . . . . .	<i>Corylus avellana</i> . . . . .	Europe (Britain), etc. . . . .	See HAZEL.
Cob nut of Jamaica . . . . .	<i>Omphalea diandra</i> . . . . .	W. Indies and Tropical America . . . . .	Food.
Coco-nut . . . . .	<i>Cocos nucifera</i> . . . . .	Tropics . . . . .	Food, oil.
Cola nut . . . . .	<i>Cola vesa</i> . . . . .	W. Africa . . . . .	Food.
Dika nut . . . . .	<i>Irvingia Barteri</i> . . . . .	W. Africa . . . . .	Food, oil.
Ginkgo nut . . . . .	<i>Ginkgo biloba</i> (seed) . . . . .	Japan, China . . . . .	Food, oil.
Hickory nut . . . . .	<i>Carya ovata</i> . . . . .	N. America . . . . .	See HICKORY.
Hog nut . . . . .	<i>Carya glabra</i> . . . . .	N. America . . . . .	Eaten by animals.
Jesuit's nut . . . . .	<i>Trapa natans</i> . . . . .	S. Europe . . . . .	Food.
Mocker nut . . . . .	<i>Carya alba glabra</i> . . . . .	N. America . . . . .	See HICKORY.
Moreton Bay chestnut . . . . .	<i>Castanospermum australe</i> . . . . .	Australia . . . . .	Food.
Nutmeg . . . . .	<i>Myristica fragrans</i> . . . . .	E. Indies . . . . .	Spice. See NUTMEG.
Nutmeg (wild) . . . . .	<i>Myristica fatua</i> , <i>M. tomentosa</i> , etc. . . . .	Tropics . . . . .	Spice. See NUTMEG.
Olive nut . . . . .	<i>Eleocarpus Ganitrus</i> , etc. . . . .	E. Indies . . . . .	Food.
Palm nut . . . . .	<i>Elaeis guineensis</i> . . . . .	W. Africa . . . . .	Oil. See PALM.
Pea nut . . . . .	<i>Arachis hypogaea</i> . . . . .	Tropics . . . . .	See PEA NUT.
Pecan nut . . . . .	<i>Carya Pecan</i> . . . . .	N. America . . . . .	Food, oil. See HICKORY.
Pekea nut . . . . .	<i>Caryocar butyrosom</i> . . . . .	Guiana . . . . .	Food.
Physic nut . . . . .	<i>Jatropha Curcas</i> . . . . .	Tropical America . . . . .	Oil.
Pine nut . . . . .	<i>Pinus Pinea</i> , etc. . . . .	Italy . . . . .	Food.
Pistachio nut . . . . .	<i>Pistacia vera</i> . . . . .	S. Europe, etc. . . . .	Food.
Quandang nut . . . . .	<i>Fusanus acuminatus</i> . . . . .	Australia . . . . .	Food.
Ravensara nut . . . . .	<i>Ravensara aromatica</i> . . . . .	Madagascar . . . . .	Spice.
Rush nut . . . . .	<i>Cyperus esculentus</i> (tubers) . . . . .	S. Europe, etc. . . . .	Food.
Sapucaia nut . . . . .	<i>Lecythis Ollaria</i> . . . . .	Brazil . . . . .	Food.
Tahiti chestnut . . . . .	<i>Inocarpus edulis</i> . . . . .	S. Sea Islands . . . . .	Food.
Walnut . . . . .	<i>Juglans regia</i> . . . . .	Asia, Europe . . . . .	Food, oil.
Water chestnut . . . . .	Species of <i>Trapa</i> . . . . .	S. Europe, India, etc. . . . .	Food.

not known commercially as nuts might with equal propriety be included in the list. Most of the nuts of real commercial importance receive separate notice, and here further allusion is only made to a few which form current articles of commerce, not otherwise treated of.

The bread nut of Jamaica is the fruit of a lofty tree, *Brosimum Alicastrum*. It is about an inch in diameter, and encloses a single seed, which, roasted or boiled, is a pleasant and nutritious article of food.

The souari or surahwa nut, called also the "butter nut of Demerara," and by fruiterers the "suwarrow nut," is the fruit of *Caryocar nuciferum*, a native of the forests of Guiana, growing 80 ft. in height. This is perhaps the finest of all the fruits called nuts. The kernel is large, soft, and even sweeter than the almond, which it somewhat resembles in taste. The few that are imported come from Demerara, and are about the size of an egg, somewhat

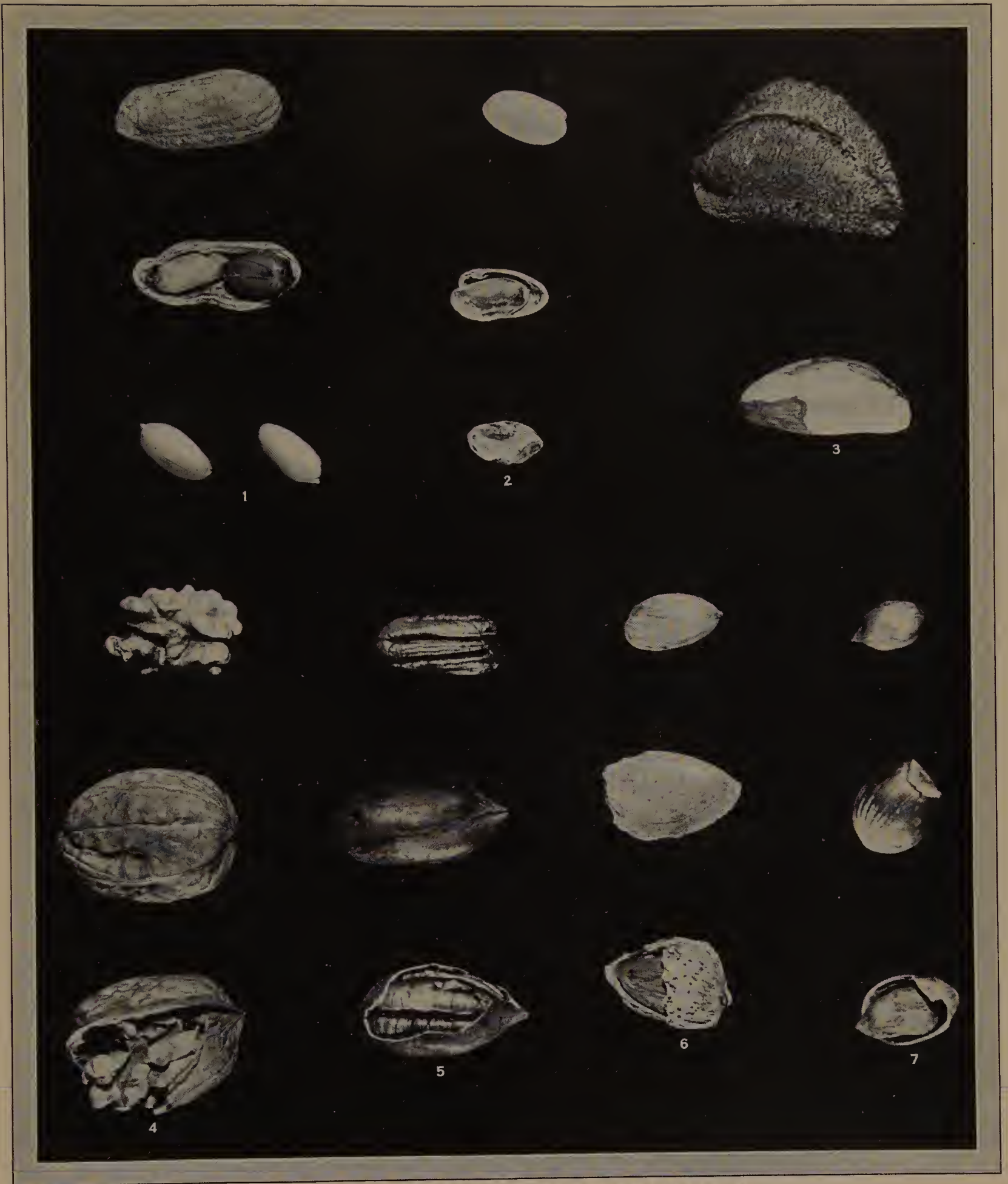
kidney-shaped, of a rich reddish-brown colour, and covered with large rounded tubercles.

Cola, kola or goora nuts are the seeds of *Cola vera* (Sterculiaceae), a tree, native of tropical Africa, now introduced into the West Indies and South America. The nuts form an important article of commerce throughout central Africa, being used over a wide area as a kind of stimulant condiment. The nuts, of which there are numerous varieties, are found to contain a notable proportion of caffeine, as much as 2.13%, besides theobromine and other important food-constituents, to which their valuable properties are due.

Coquilla nuts, the hard inner portion ("stone") of the palm, *Attalea funifera*, the piassaba of Brazil, are highly valued for turnery purposes. They have an elongated oval form, 3 to 4 in. in length, and being intensely hard they take a fine polish, displaying a richly streaked brown colour.

Name	Source	Locality	Remarks
Betel nut . . . . .	<i>Areca Catechu</i> . . . . .	E. Indies . . . . .	Necklaces.
Bladder nut . . . . .	<i>Staphylea pinnata</i> . . . . .	S. Europe . . . . .	Tanning.
Boomah nut . . . . .	<i>Pycnocomia macrophylla</i> . . . . .	Africa . . . . .	Medicine, beads.
Bonduc nut . . . . .	<i>Caesolpinia Bonduc</i> . . . . .	India . . . . .	Clearing dirty water.
Clearing nut . . . . .	<i>Strychnos potatorum</i> . . . . .	India . . . . .	Turnery.
Coquilla nut . . . . .	<i>Attalea funifera</i> . . . . .	Brazil . . . . .	See PALM.
Corozo nut or vegetable ivory . . . . .	<i>Phytelephas macrocarpa</i> . . . . .	Tropical S. America . . . . .	Perfume.
Cumara nut (Tonka or Tonquin bean) . . . . .	<i>Dipteryx odorata</i> . . . . .	S. America . . . . .	Beads.
Grugru nut . . . . .	<i>Acrocomia selerocarpa</i> . . . . .	S. Europe . . . . .	Starch.
Horse chestnut . . . . .	<i>Aesculus Hippocastanum</i> . . . . .	E. Indies . . . . .	Marking ink and varnish.
Marking nut . . . . .	<i>Semecarpus Anacardium</i> . . . . .	Levant . . . . .	Dyeing and ink making. See GALLS.
"Nut" galls . . . . .	<i>Quercus galls</i> . . . . .	E. Indies . . . . .	Medicine. See NUX VOMICA.
Poison nut . . . . .	<i>Strychnos Nux-Vomica</i> . . . . .	S. America . . . . .	Aromatic.
Sassafras nut . . . . .	<i>Nectandra Puchury</i> . . . . .	S. America . . . . .	Curiosity.
Snake nut . . . . .	<i>Ophiocaryon paradoxum</i> . . . . .	W. Indies . . . . .	Washing; ornamental.
Soap nut . . . . .	<i>Sapindus Saponaria</i> . . . . .		





## VARIOUS KINDS OF COMMERCIAL AND EDIBLE NUTS

READ FROM TOP TO BOTTOM

1. Peanut; half of shell removed exposing, left, kernel, and right, kernel enclosed in skin; two whole kernels
2. Pistachio nut; half of shell removed showing kernel; kernel removed from shell
3. Brazil nut; whole kernel
4. Walnut kernel; whole walnut; shell broken to expose part of kernel
5. Pecan kernel; whole pecan nut; shell broken showing kernel
6. Almond kernel; whole almond; shell broken showing part of kernel
7. Filbert kernel; whole filbert; part of shell removed to show kernel







The marking nut, *Semecarpus Anacardium*, is a fruit closely allied in its source and properties to the cashew nut (*q.v.*). The marking nut is a native of the East Indies, where the extremely acrid juice of the shell of the fruit in its unripe state is mixed with quicklime and used as a marking-ink. The juice when dry is the basis of a valuable caulking material and black varnish. The seeds are edible, and the source of a useful oil.

Physic nuts are the produce of the euphorbiaceous tree, *Jatropha Curcas*, whence a valuable oil, having similar purgative properties to castor oil, is obtained. The plant is a native of South America, but is found in all tropical countries.

Pine nuts are the seeds of several species of *Pinus*, eaten in the countries of their growth, and also serving to some extent as sources of oil. Of these the most important are the stone pine, *Pinus Pinea*, of Italy and the Mediterranean coasts, and the Russian stone pine, *Pinus Cembra*. *Pinus Sabiniana*, the digger pine of California; *P. edulis*, *P. monophylla*, *P. Parryana*, and *P. cembroides*, the "piñons" of the southwestern United States and northern Mexico; and also *P. Gerardiana* of the Himalayas similarly yield edible seeds. These seeds possess a pleasant, slightly resinous flavour.

Ravensara nuts, the fruit of *Ravensara aromatica* (Lauraceae), a native of Madagascar, is used as a spice under the name of the Madagascar clove nutmeg.

The Sapucaia nut is produced by a large tree, *Lecythis Ollaria*. Its specific name is taken from the large urn-shaped capsules, called "monkey-pots" by the inhabitants, which contain the nuts. The sapucaya nut has a sweet flavour, resembling the almond, and is of a rich amber-brown; not unlike the Brazil nut.

Soap nuts are the fruits of various species of *Sapindus*, especially *S. saponaria*, natives of tropical regions. They are so called because their rind or outer covering contains saponin, which lathers in water, and so is useful in washing.

**SEED.** The seed is formed from the ovule as the result of fertilization (*q.v.*). It is contained in a seed vessel (*see* FRUIT)

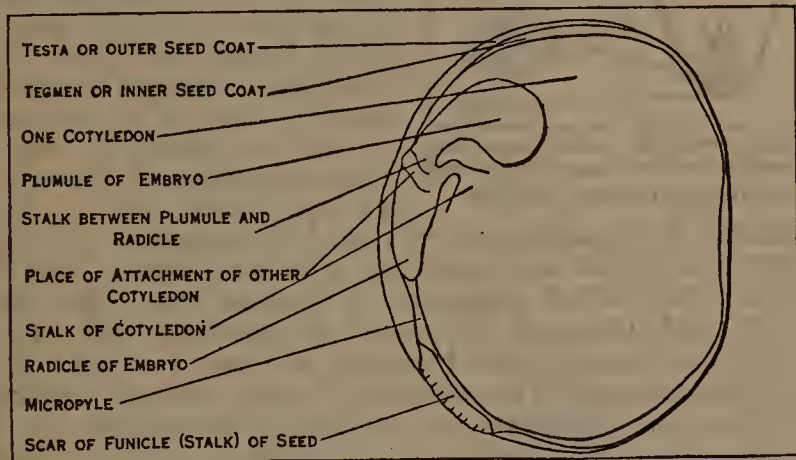


FIG. 1.—SEED OF PEA (*PISUM SATIVUM*) WITH ONE COTYLEDON REMOVED

formed from the ovaries in the plants called *angiospermous*; while in *gymnospermous* plants, such as Coniferae and Cycadaceae, it is naked, or, in other words, has no true pericarp. It sometimes happens in angiosperms, that the seed-vessel is ruptured at an early period of growth, so that the seeds become more or less exposed during their development; this occurs in *mignonette*, where the capsule opens at the apex, and in *Cuphea*, where the placenta bursts through the ovary and floral envelopes, and appears as an erect process bearing the young seeds. After fertilization the ovule is greatly changed as a result of the formation of the embryo. In the embryo-sac of most angiosperms (*q.v.*) there is a development of cellular tissue, the endosperm, more or less filling the embryo-sac. In gymnosperms (*q.v.*) the endosperm or embryo sac tissue is formed preparatory to fertilization. The fertilized egg enlarges and forms the embryo. The embryo-



FIG. 2.—SEED OF ASCLEPIAS WITH CLUSTER OF HAIRS ARISING FROM EDGES OF MICROPYLE

sac enlarges greatly, displacing gradually the surrounding nucellus, which eventually forms merely a thin layer around the sac, or completely disappears. The remainder of the nucellus and the integuments of the ovules form the seed-coats. In some cases a delicate inner coat or *tegmen* can be distinguished from a tougher outer coat or *testa*; often, however, the layers are not thus separable. The consistency of the seed-coat, its thickness, the character of its surface, etc., vary widely, the variations being

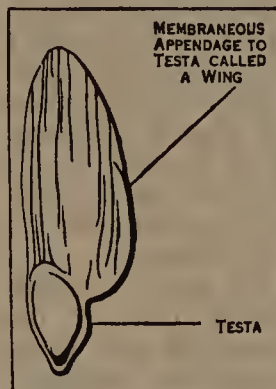


FIG. 3.—SEED OF PINE (*PINUS*)

often closely associated with the means of seed-dispersal. An account of the development of the seed from the ovule will be found in the article *ANGIOSPERMS*. When the pericarp is dehiscent the seed-covering is of a strong and often rough character; but when the pericarp is indehiscent and encloses the seed for a long period, the outer seed-coat is thin and soft. The cells of the testa are often coloured, and have projections and appendages of various kinds. Thus in *Abrus precatorius*, it is a bright red; in French beans it is beautifully mottled; in *Asclepias* it has hairs attached to it; and in *Bignonia* and the pines and firs it is expanded in the form of wing-like appendages. In *Collomia* and other seeds, it contains spiral cells, from which, when moistened with water, the fibres uncoil in a beautiful manner; and in flax (*Linum*) and others the cells swell up and become mucilaginous. These structural peculiarities of the testa in different plants have relation to the scattering of the seed. But in some plants the pericarps subserve the same purpose; this especially occurs in small pericarps enclosing single seeds, as achenes, caryopsides, etc. Thus in *Compositae*, the pappose limb of the calyx forms a parachute to the pericarp; and the epicarp is prolonged as a wing in *Fraxinus* and *Acer*.

Sometimes there is an additional covering to the seed, formed after fertilization, to which the name *arillus* has been given. This is seen in the passion-flower. In the nutmeg this additional coat constitutes a lacinated scarlet covering called *mace*. The fleshy

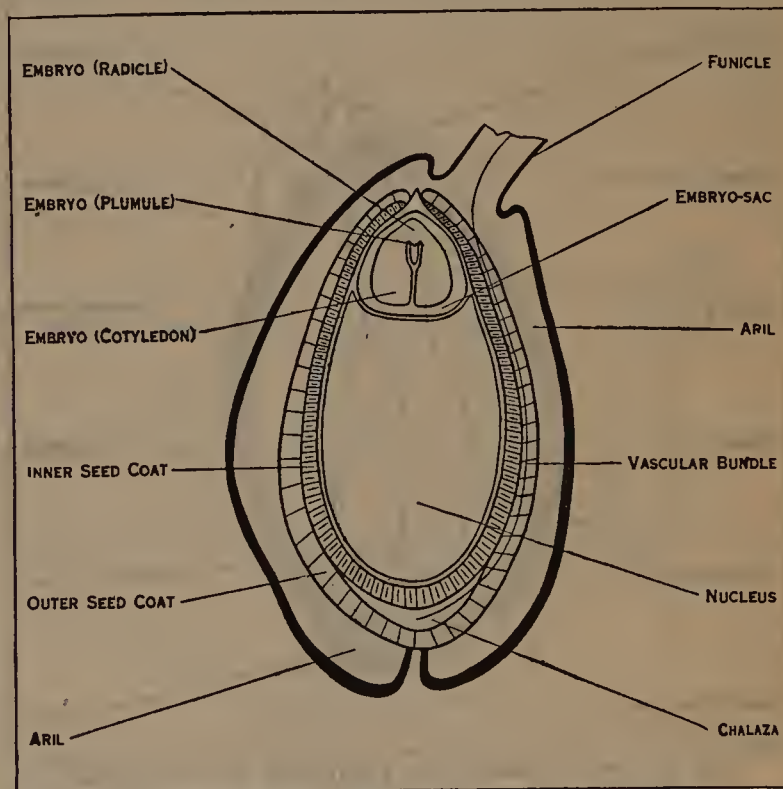


FIG. 4.—YOUNG ANATROPAL SEED OF THE WHITE WATER LILY (*NYMPHAEA ALBA*), CUT VERTICALLY

scarlet covering formed around the naked seed in the yew is by some considered of the nature of an aril. On the testa, at various points, there are produced at times other small outgrowths to which the name *caruncles* has been given. The funicles of the ovules frequently attain a great length in the seed, and in some magnolias, when the fruit dehisces, they appear as long scarlet



cords suspending the seeds. The hilum or umbilicus of the seed is usually well marked, as a scar of varying size; in the calabar bean it extends along a large portion of the edge of the seed; it frequently exhibits marked colours, being black in the bean, white in many species of *Phaseolus*, etc. The *micropyle* of the seed may be recognizable by the naked eye, as in the pea and bean tribe, etc., or it may be minute or microscopic. It indicates the true apex of the seed, and is important as marking the point to which the root of the embryo is directed.

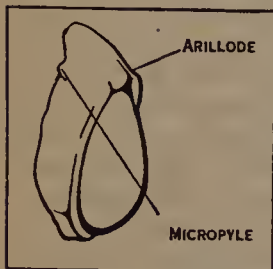


FIG. 5.—ARILLODE, OR FALSE ARIL, OF THE SPINDLE-TREE (*EUONYMUS*) ARISING FROM THE MICROPYLE

The position of the seed as regards the pericarp resembles that of the ovule in the ovary, and the same terms are applied—erect, ascending, pendulous, suspended, curved, etc. These terms have no reference to the mode in which the fruit is attached to the axis. Seeds exhibit great varieties of form. They may be flattened laterally (*compressed*), or from above downwards (*depressed*). They may be round, oval, triangular, polygonal, rolled up like a snail, as in *Physostemon*, or coiled up like a snake, as in *Ophiocaryon paradoxum*.

The endosperm formed in the embryo-sac of angiosperms after fertilization, and found previous to it in gymnosperms, consists of cells containing nitrogenous and starchy or oily material, destined for the nutriment of the embryo. It occupies the whole cavity of the embryo-sac, or is formed only at certain portions of it, at the apex, as in *Rhinanthus*, at the base, as in *Vaccinium*, or in the middle, as in *Veronica*. As the endosperm increases in size along with the embryo-sac and the embryo, the substance of the original nucellus of the ovule is gradually absorbed. Some-

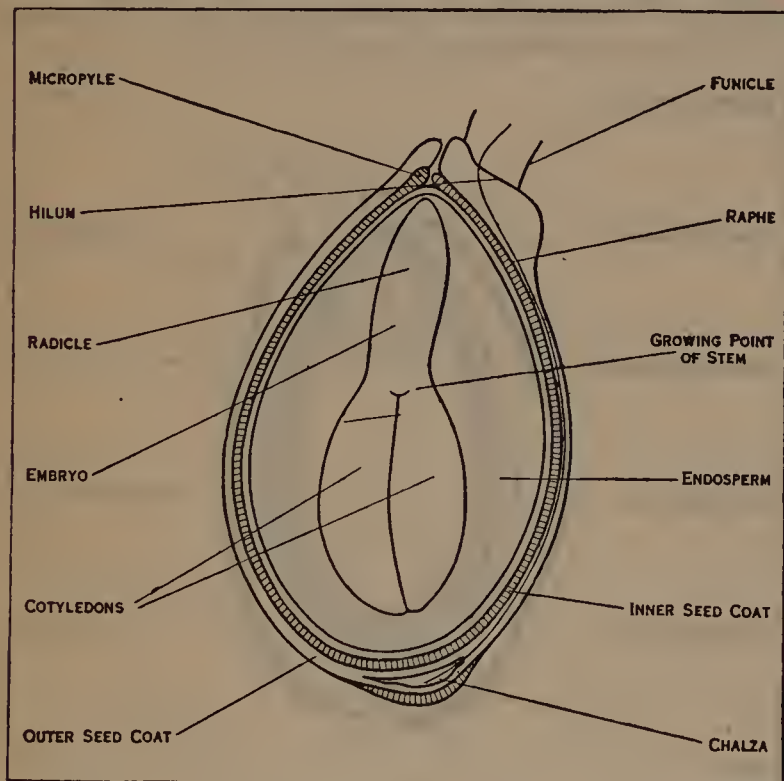


FIG. 6.—SEED OF PANSY (*VIOLA TRICOLOR*) CUT VERTICALLY

times, however, as in Zingiberaceae, no endosperm is formed; the cells of the original nucellus, becoming filled with food-materials for the embryo, are not absorbed, but remain surrounding the embryo-sac with the embryo, and constitute the *perisperm*. Again, in other plants, as Nymphaeaceae, both endosperm and perisperm are present. There is a large class of plants in which although at first after fertilization a mass of endosperm is formed, yet, as the embryo increases in size, the nutrient matter from the

endospermic cells passes out from them, and is absorbed by the cells of the embryo plant. In the mature seed, in such cases, there is no separate mass of tissue containing nutrient food-material apart from the embryo itself. Such a seed is said to be *exalbuminous*, as in most Leguminosae. When either endosperm or perisperm or both are present the seed is said to be *albuminous*.

The albumen varies much in its nature and consistence, and furnishes important characters. It may be farinaceous or mealy,

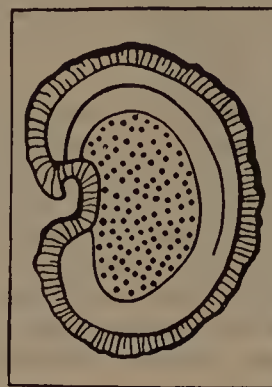


FIG. 7.—SEED OF RED CAMPION (*LYCHNIS*), CUT VERTICALLY

consisting chiefly of cells filled with starch, as in cereal grains, where it is abundant; fleshy or cartilaginous, consisting of thicker cells which are still soft, as in the coco-nut, and which sometimes contain oil, as in the oily albumen of *Ricinus* and poppy; horny, when the cell-walls are slightly thickened and capable of swelling, as in date and coffee; the cell-walls sometimes become greatly thickened, filling up the testa as a hard mass, as in vegetable ivory (*Phytelphas*). A cavity is sometimes left in the centre which is usually filled with fluid, as in the coco-nut. The relative size of the embryo and of the endosperm varies much.

In monocotyledons the embryo is usually small, and the endosperm large, and the same is true in the case of coffee and many other dicotyledons. The opposite is the case in other plants, as in the Labiatae.

The embryo consists of an axis bearing the *cotyledons* or the first leaves of the plant. To that part of this axis immediately beneath the cotyledons the term *hypocotyl* has been applied, and continuous backwards with it is the young root or *radicle*, the

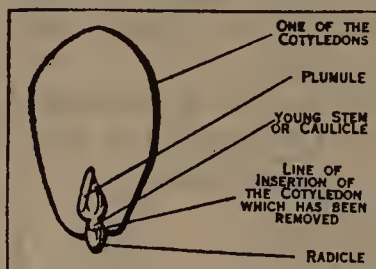


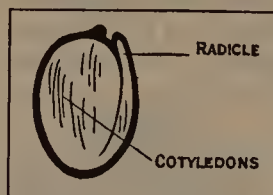
FIG. 8.—MATURE DICOTYLEDONOUS EMBRYO OF THE ALMOND WITH ONE OF THE COTYLEDONS REMOVED

descending axis, their point of union being the collar or neck. The terminal growing bud of the axis is called the *plumule*, and represents the ascending axis. The radicular extremity points towards the micropyle, while the cotyledonary extremity is pointed towards the base of the ovule or the chalaza. Hence, by ascertaining the position of the micropyle and chalaza, the two extremities of the embryo can in general be discovered. It is in many cases difficult to recognize the parts in an embryo; thus in *Cuscuta*, the embryo appears as an elongated axis without divisions; and in *Caryocar* the mass of the embryo is made up by the radicular extremity and hypocotyl, in a groove of which the cotyledonary extremity lies embedded. In some monocotyledonous embryos, as in Orchidaceae, the embryo is undifferentiated, being a mere cellular mass showing no parts. When the embryo follows the direction of the axis of the seed, it is axile or axial; when it

is not in the direction of the axis, it becomes abaxile or abaxial. In campylotropous seeds the embryo is curved, and in place of being embedded in endosperm, is frequently external to it.

It has been already stated that the radicle of the embryo is directed to the micropyle, and the cotyledons to the chalaza. In some cases, by the growth of the integuments, the former is turned round so as not to correspond with the apex of the nucellus, and then the embryo has the radicle directed to one side, and is called *excentric*, as is seen in Primulaceae and many palms, especially the date. The position of the embryo in different kinds of seeds varies. In an orthotropal seed the embryo is inverted or *antitropal*, the radicle pointing to the apex of the seed, or to the part opposite the hilum. Again, in an anatropal seed the embryo is erect or *homotropal*, the radicle being directed to the base of the seed. In curved or campylotropal seeds the embryo is folded so that its radicular and cotyledonary extremities

FIG. 9.—EXALBUMINOUS SEED OF WALLFLOWER (*CHEIRANTHUS*), CUT VERTICALLY





are approximated, and it becomes *amphitropal*. In this instance the seed may be exalbuminous, and the embryo may be folded on itself; or albuminous, the embryo surrounding more or less completely the endosperm and being peripheral. According to the mode in which the seed is attached to the pericarp, the radicle may be directed upwards or downwards, or laterally, as regards the ovary. In an orthotropal seed attached to the base of the pericarp it is superior as also in a suspended anatropal seed. In other anatropal seeds the radicle is inferior. When the seed is horizontal as regards the pericarp, the radicle is either centrifugal, when it points to the outer wall of the ovary; or centripetal, when it points to the axis or inner wall of the ovary. These characters are of value for classification, as they are often constant in large groups of genera.

Plants in which there are two cotyledons formed in the embryo are *dicotyledonous*. The two cotyledons thus formed are opposite to each other, but are not always of the same size. Thus, in the Nyctaginaceae, one of them is smaller than the other (often very small), and in *Carapa guianensis* there appears to be only one, in consequence of the intimate union which takes place between the two. The union between the cotyledonary leaves may continue after the young plant begins to germinate. The texture of the cotyledons varies. They may be thick, as in the pea, exhibiting no traces of venation, with their flat internal surfaces in contact, and their backs more or less convex; or they may be in the form of thin and delicate laminae, flattened on both sides, and having distinct venation, as in *Euonymus*, etc. The cotyledons usually form the greater part of the mature embryo, and this is remarkably well seen in such exalbuminous seeds as the bean and pea.

Cotyledons are usually entire and sessile. But they occasionally become lobed, as in the walnut; or petiolate, as in *Geranium molle*; or auriculate, as in the ash. Like leaves in the bud, cotyledons may be either applied directly to each other, or may be folded in various ways, the same terms being applied as to the foliage leaves. The radicle and cotyledons are either straight or variously curved. Thus, in some cruciferous plants, as the wallflower, the cotyledons are applied by their faces, and the radicle is folded on their edges, so as to be lateral; the cotyledons are here *accumbent*. In others, as *Hesperis*, the cotyledons are applied to each other by their faces, and the radicle is folded on their back, so as to be dorsal, and the cotyledons are *incumbent*. Again, the cotyledons are *conduplicate* when the radicle is dorsal, and enclosed between their folds. In other divisions the radicle is folded in a spiral manner, and the cotyledons follow the same course.

In many gymnosperms more than two cotyledons are present, and they are arranged in a whorl. This occurs in Coniferae, especially in the pine, fir, spruce and larch, in which six, nine, twelve and even fifteen have been observed; they resemble in their form and mode of development the clustered or fasciculated leaves of the larch. In species of *Streptocarpus* the cotyledons are permanent, and act the part of leaves. One of them is frequently largely developed, while the other is small or abortive.

In those plants in which there is only a single cotyledon in the embryo, hence called *monocotyledonous*, the embryo usually has a cylindrical form more or less rounded at the extremities, or elongated and fusiform, often oblique. The axis is usually very short compared with the cotyledon, which in general encloses

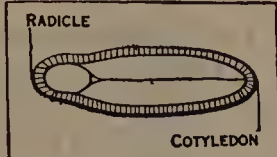


FIG. 10.—TRANSVERSE SECTION OF SEED OF WALLFLOWER, WITH RADICLE FOLDED ON EDGES OF ACCUMBENT COTYLEDONS

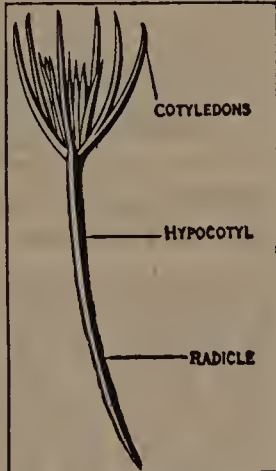


FIG. 11.—POLYCOTYLEDONOUS EMBRYO OF THE PINE (PINUS), BEGINNING TO SPROUT

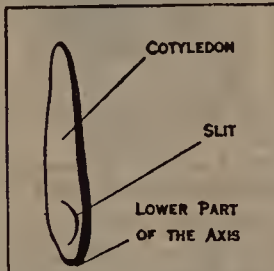


FIG. 12.—EMBRYO OF A SPECIES OF ARROW-GRASS

the plumule by its lower portion, and exhibits on one side a small slit which indicates the union of the edges of the vaginal or sheathing portion of the leaf. In grasses, by the enlargement of the embryo in a particular direction, the endosperm is pushed on one side, and thus the embryo comes to lie outside at the base of the endosperm. The lamina of the cotyledon is not developed.

Upon the side of the embryo next the endosperm and enveloping it is a large shield-shaped body, termed the *scutellum*. This is an outgrowth from the base of the cotyledon, enveloping more or less the cotyledon and plumule, in some cases, as in maize, completely investing it; in other cases, as in rice, merely sending small prolongations over its anterior face at the apex. (See GRASSES.) In many aquatic monocotyledons (e.g., *Potamogeton*) there is a much-developed hypocotyl, which forms the greater part of the embryo and acts as a store of nutriment in germination. In some grasses, as oats, a projection of cellular tissue is seen upon the side of the embryo opposite to the scutellum, that is, on the anterior side. This has been termed the *epiblast*. This by some was considered the rudimentary second cotyledon; but is now generally regarded as an outgrowth of the sheath of the true cotyledon.

**ROOT**, in popular use, the part of a plant which is normally below the surface of the earth. Botanically its application is more restricted. The embryo of a typical plant, for instance a pea plant, has an ascending axis which grows into the shoot, and a descending axis or radicle which grows into the root. When the seed germinates, the radicle is the first to appear; it grows downwards, and its primary function is to act as a hold-fast for the plant; its most important function, however, is the absorption of water and dissolved nutrient substances from the soil, and it also frequently serves for storage of foodstuffs. The root is distinguished from underground shoots by not bearing leaves and by having its

apex (growing point) protected by a cap (root-cap), which can be clearly seen by making a median vertical section through the root-tip; the cap protects it in its passage through the soil. The root also generally bears root-hairs, slender unicellular outgrowths of the outer layer, borne in the region a little behind the root-tip. The root-hairs serve to increase the surface of the root for absorption of water and mineral substances; they also are of service in bringing the root into intimate relationship with the soil particles; the older root-hairs are continually dying off, so that they are borne only on a small part of the area behind the apex. Branches of the root, which repeat the form and structure of the main root, are developed in regular succession from above downwards (acropetal), and owing to the fact that they originate in a definite position in the interior of the root (generally opposite the xylem masses) they develop in longitudinal rows and have to break through the overlying tissue of the parent root. True forking of the root (dichotomy) occurs in the Lycopodiaceae (the shoots of which also branch dichotomously), but is unknown in the higher plants.

Roots which originate elsewhere than as acropetal outgrowths of a main root are known as *adventitious*, and may arise on any part of a plant. They are especially numerous on underground

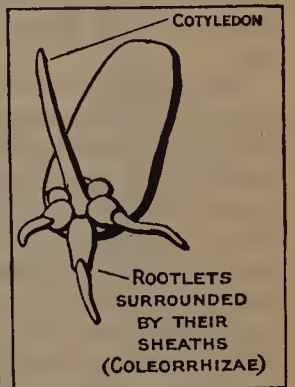


FIG. 13.—GRAIN OF WHEAT (TRITICUM) GERMINATING

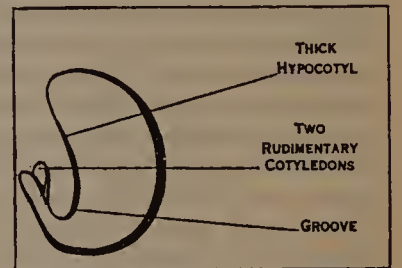
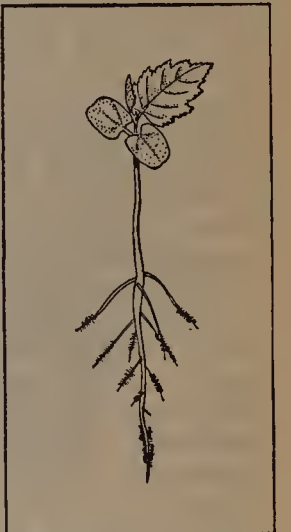


FIG. 14.—EMBRYO OF CARYOCAR



FROM STRASBURGER'S "LEHR-BUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 1.—SEEDLING (ULTIMATE ROOT-BRANCHES)



stems, such as the under side of rhizomes, and also develop from stem nodes under favourable conditions, such as moisture and absence of light; a young shoot or a cutting placed in moist soil quickly forms adventitious roots. They may also arise from leaves under similar conditions, as, for instance, from begonia leaves when planted in soil.

The forms of roots depend on their shape and mode of branching. When the central axis goes deep into the ground in a tapering manner without dividing, a *tap-root* is produced. This kind of root is sometimes shortened, and becomes swollen by storage of food-stuffs, forming the *conical* root of carrot, or the *fusiform* or spindle-shaped root of radish, or the *napiform* root of turnip. In ordinary forest trees the first root protruded continues to elongate and forms a long primary root-axis, whence secondary axes come off. In primary plants, especially monocotyledons, the primary axis soon dies and the secondary axes takes its place. When the descending axis is very short, and at once divides into thin, nearly equal fibrils, the root is called *fibrous*, as in many grasses; when the fibrils are thick and succulent, the root is *fasciculated*, as in *Ranunculus Ficaria*, and *Oenanthe crocata*; when some of the fibrils are developed in the form of tubercles, the root is *tuberculate*, as in dahlia. Some of these so-called roots are formed of a stem and root combined, as in *Orchis*, where the tuber consists of a fleshy swollen root bearing at the apex a stem bud. As in the case of the stem, growth in length occurs only for a short distance behind the apex, but in long-lived roots increase in diameter occurs continually in a similar manner to growth in thickness in the stem.

Roots are usually underground and colourless, but in some cases where they arise from the stem they pass for some distance through the air before reaching the soil. Such roots are called *aerial*. They are well seen in the screw-pine (*Pandanus*), the Banyan (*Ficus indica*), and many other species of *Ficus*, where they assist in supporting the stem and branches. In the mangrove they often form the entire support of the stem, which has decayed at its lower part. In tree-ferns they form a dense coating around, and completely concealing, the stem; such is also the case in some *Draenas* and palms. In *epiphytes*, or plants growing in the air, attached to the trunks of trees, such as orchids of warm climates, the aerial roots produced do not reach the soil; they continue always aerial and greenish, and they possess stomata. Delicate hairs are often seen on these epiphytal roots, as well as a peculiar spongy investment formed by the cells of the epidermis which have lost their succulent contents and are now filled with air. This layer is called the *velamen*, and serves to condense the moisture contained in the air, on which the plant is dependent for its water-supply. Some leafless epiphytic orchids, such as species of *Angraecum*, depend entirely upon their aerial roots for nourishment; these perform the functions both of leaves and roots. A respiratory or aerating function is performed by roots of certain mangroves (*q.v.*), growing in swampy soil or water and sending vertical roots up into the air which are provided with aerating passages by which the root system below can communicate with true outside air.

Parasitic plants, as the mistletoe (*Viscum*), broom-rape (*Orobanche*), dodder (*Cuscuta*) and *Rafflesia*, send root-like processes into the substance of the plants whence they derive nourishment. Leaf-buds are sometimes formed on roots, as in plum, cherry

and other fruit trees; the common elm affords an excellent example, the young shoots which grow up in the neighbourhood of a tree arising from the roots beneath the soil. In some plants no roots are formed at all; thus in the orchid *Corallorhiza*, known as coral-root, a stem-structure, the shortly branched underground rhizome, performs all the functions of a true root, which is absent. In aquatic plants the root acts merely as a holdfast or it is altogether absent as in *Salvinia*, *Utricularia* and various other aquatic plants. The well known epiphyte *Tillandsia usneoides* (Spanish moss) is rootless.

For the interval structure of a root see PLANTS: *Anatomy*.

**STEM**, in popular language the stalk of a plant or trunk of a tree. In botany a stem may be defined as an axis bearing leaves. The stem with its leaves is known as the shoot. Structurally it differs from a root in having no cap (*root cap*) over the growing-point and in terminating in a bud. Under the term *caulome* (stem-structure) are included all those parts of a plant morphologically equivalent in bearing leaves. The stem generally ascends, seeking air and light, and has therefore been termed the *ascending axis*. Stems have usually considerable firmness and solidity, but sometimes they are weak, and either lie prostrate on the ground, thus becoming *procumbent*, or climb on plants and rocks by means of rootlets, like the ivy, being then called *scandent*, or twist round other plants in a spiral manner like woodbine, when they are *twining*. Twining plants turn either anti-clockwise, as the French

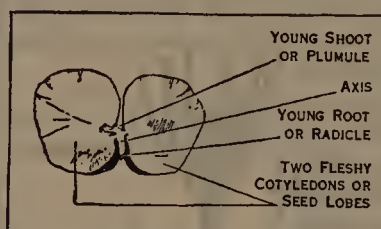
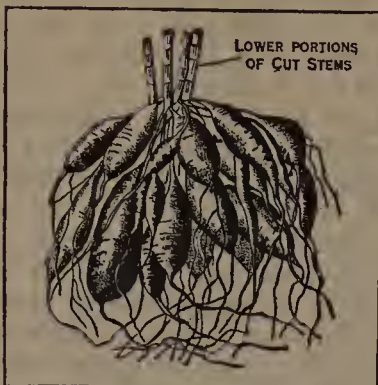


FIG. 1.—EMBRYO OF BEAN WITH COTYLEDONS SEPARATED

bean, convolvulus, dodder and gourd; or clockwise, as honeysuckle, twining polygonum, hop and black bryony. In other cases climbing plants are supported by tendrils, which may be modified stems, as in vine, bryony, passion-flower, or by the tendril-like leaf-stalks, as in clematis and *Tropaeolum*. In warm climates twining plants (*lianas*) often form thick woody stems, while in temperate regions they are generally herbaceous. Some stems are developed more in diameter than in height, and present a peculiar shortened and thickened aspect, as *Testudinaria* or tortoise-plant, cyclamen, *Melocactus*, *Echinocactus* and other *Cactaceae*; while in many orchids the stem assumes an oval or rounded form, and is called a *pseudobulb*.

Names are given to plants according to the nature and duration of their stems. *Herbs*, or *herbaceous* plants, have stems which die down annually. In some of them the whole plant perishes after flowering; in others, the lower part of the stem forming the *crown of the root* remains, bearing buds from which the stem arises next season. In *biennial* herbs the whole plant perishes after two years, while in *perennial* herbs the crown is capable of producing stems for many years, or new annual products are repeatedly added many times, if not indefinitely, to the old stems. The short permanent stem of herbaceous plants is covered partially or completely by the soil, so as to protect the buds. Plants producing permanent woody stems are called *trees* and *shrubs*. The latter produce branches from or near the ground, while the former have conspicuous trunks. Shrubby plants of small stature are called *under-shrubs* or *bushes*. The limits between these different kinds of stem are not always well defined; and there are some plants which occupy an intermediate position between the shrubs on the one hand and the trees on the other, sometimes called *arborescent shrubs*.

The stem is not always conspicuous. Plants with a distinct stem are *caulescent*; those in which it is inconspicuous are *acaulescent*, as the primrose, cowslip and dandelion. A similar term is given



FROM STRASBURGER'S "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)  
FIG. 2.—ROOT-TUBERS OF DAHLIA VARIABILIS

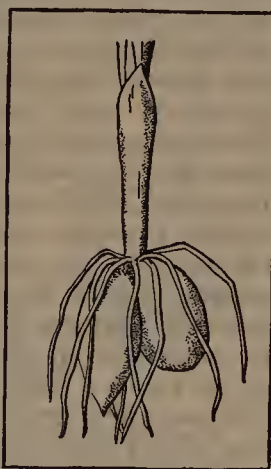
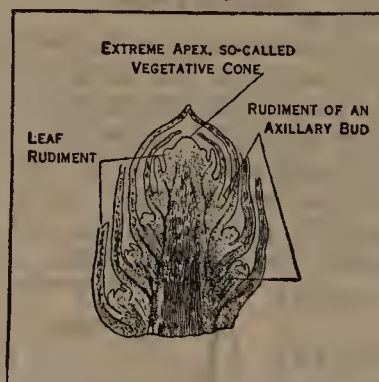


FIG. 3.—FLESHY ROOT OF ORCHIS



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (FISCHER)  
FIG. 2.—APEX OF SHOOT OF PHANEROGAMIC PLANT STEM



in ordinary language to plants whose stems are buried in the soil, such as cyclamen or sowbread. Some plants are truly stemless, and consist only of expansions of cellular tissue representing stem and leaf, called a *thallus*, and hence are denominated *Thallophytes*. (See ALGAE, FUNGI.)

**Development of Stem.**—The first rudiment of the young shoot of the embryo appears from the seed after the radicle (young root) has protruded. It is termed the *plumule*, and differs from the radicle in the absence of a root-cap and in its tendency to ascend. The apical growing portion constitutes the terminal bud of the plant, and by its development the stem increases in height; projections appear at regular intervals, which are the rudimentary leaves, and in addition there is a provision for the production of lateral buds, which develop into lateral shoots more or less re-



FIG. 3.—LEAF-BUD OF SYCAMORE

sembling the parent stem, and by these the branching of the plant is determined. These buds are found in the *axil* of previously formed leaves; or, in other words, in the angle formed between the stem and leaf. They are hence called *axillary*. They are produced like the leaves from the outer portion of the stem, and at first consist entirely of cellular tissue, but in the progress of growth vascular bundles are formed in them continuous with those of the stem, and ultimately branches are produced, which in every respect resemble the axis whence the buds first sprang. The place of origin of the leaf is called a *node*; the intervals between nodes are called *internodes*. The stem, although it has a tendency to rise upwards when first developed, in many instances becomes prostrate, and either lies along the ground partially covered by the soil, or runs completely underneath its surface, giving off roots from one side and buds from the other. Some stems are therefore subterranean, and are distinguished from roots by the provision made for regular leaf-buds.

**Growth and Bud Formation.**—Growth in length of the stem is due to elongation of the internodes; the zone of most rapid growth is at some distance below the apex; below this the rate of growth gradually diminishes until the portion is reached where growth in length no longer takes place. In some cases, as in the stems of grasses, growth in length persists for a longer time in a small region at the base of the internodes; this is known as *intercalary* growth. In the dwarf or short shoots, such as those of the larch, the internodes do not elongate and the leaves remain close together. Lateral buds give rise to *branches*, from which others, called *branchlets* or *twigs*, arise. The terminal bud, after producing leaves, sometimes dies at the end of one season, and the whole plant, as in annuals, perishes; or part of the axis is persistent, and remains for two or more years, each of the leaves before its decay producing a bud in its axil. This bud continues the growth in spring. In ordinary trees, in which there is provision made for the formation of numerous lateral buds, any injury done to a few branches is easily repaired; but in palms, which only form terminal buds, and have no provision for a lateral formation of them, destruction of the terminal bud may kill the tree. In the trees of temperate and cold climates the buds which are developed during one season lie dormant during the winter, ready to open in the spring. They are generally protected by external modified leaves in the form of *scales*, which frequently exhibit a firmer and coarser texture than the leaves themselves. They serve a temporary purpose, and usually fall off sooner or later, after the leaves are expanded. The bud is often protected by a coating of resinous matter, as in the horse-chestnut and balsam poplar, or by a thick downy covering, as in the willow.

In plants of warm climates the buds are often formed by the ordinary leaves without any protecting appendages; such buds are called *naked*. A bud may be removed in a young state from one

plant and grafted upon another by the process of *budding*, so as to continue to form its different parts; and it may even be made to grow in the soil, in some instances, immediately after removal. In some trees of warm climates, as papaw, palms and tree-ferns, growth by terminal buds is well seen.

When the terminal bud is injured or arrested in its growth the elongation of the main axis stops, and the lateral branches often acquire increased activity. By continually cutting off the terminal buds or branches, a woody plant is made to assume a bushy appearance, and thus *pollard* trees are produced. The peculiar bird-nest appearance often presented by the branches of the common birch depends on an arrestment in the terminal buds, a shortening of the internodes, and a consequent clustering or fasciculation of the twigs. (See GALLS.)

**Branching.**—The mode in which branches come off from the stems gives rise to various forms of trees, as pyramidal, spreading or weeping—the angles being more or less acute or obtuse. In the Italian poplar and cypress the branches are erect, forming acute angles with the upper part of the stem; in the oak and cedar they are spreading or patent, forming nearly a right angle; in the weeping ash and elm they come off at an obtuse angle; while in the weeping willow and birch they are pendulous from their flexibility. The comparative length of the upper and under branches also gives rise to differences in the contour of trees, as seen in the conical form of spruce, and the umbrella-like form of the Italian or stone pine (*Pinus Pinea*).

Branches are sometimes long and slender, and run along the ground, producing buds with roots and leaves at their extremity. This is seen in the *runner* of the strawberry. In the houseleek (*Sempervivum*) there is a similar prostrate branch of a shorter and thicker nature, known as an *offset*, producing a bud at its extremity capable of independent existence. In many instances the branch decays, and the young plant assumes a separate existence. Gardeners propagate plants by the process of *layering*, which consists in bending a twig, fixing the central part of it into the ground, and, after the production of roots, cutting off its connection with the parent. A *stolon* differs from these in being a branch which curves towards the ground, and, on reaching a moist spot, takes root and forms an upright stem, and ultimately a separate plant. This is a sort of natural layering, and the plant producing such branches is called *stoloniferous*. In the rose and mint a subterranean branch arises from the stem, which runs horizontally to a certain extent, and ultimately sends up an aerial stem, which becomes an independent plant. Such branches are denominated *suckers*, and the gardener cuts the connection between the sucker and the parent stem, to propagate these plants.

In the case of asparagus and other plants which have a perennial stem below ground, subterranean buds are annually produced which appear above ground as shoots or branches covered with scales at first, and ultimately with true leaves. These branches are herbaceous and perish annually, while the true stem remains below ground ready to send up fresh shoots next season. In bananas and plantains the apparent aerial stem is a shoot sent up by an underground stem, and perishes after fruiting. Branches are sometimes arrested in their development, and, in place of forming leaves, become transformed into *spines* or *thorns*, as in the hawthorn. Plants which have spines in a wild state, as the apple

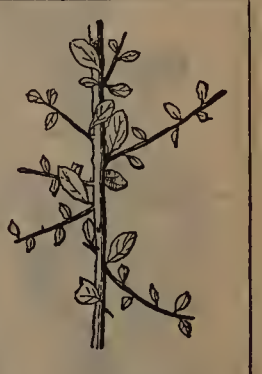


FIG. 5.—BRANCH OF SLOE



FIG. 4.—TRANSVERSE SECTION OF SYCAMORE LEAF-BUD



FIG. 6.—TWIG OF BUTCHER'S BROOM



and pear, often lose them when cultivated, in consequence of their being changed into branches; in some cases, as in the sloe (*Prunus spinosa*), a branch bears leaves at its lower portion, and terminates in a spine. In some cases branches become flat and leaf-like, taking the place in the plant economy of the leaves, which are reduced to small scales or spines, as in butcher's broom; branches showing this modification are termed cladodes or phylloclades. In Cactaceae (e.g., *Opuntia*, prickly pear) and fleshy euphorbias, where the leaves are reduced to spines, the fleshy stems become green and perform the functions of leaves; they also serve as water reservoirs for the plants, which are natives of very dry countries.



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (FISCHER)  
FIG. 7.—*OPUNTIA MONACANTHA*

**Rhizomes, Corms and Bulbs.**—The typical form of stems is rounded. They are sometimes compressed or flattened laterally, while at other times they are angular. Various terms are applied to the forms of stems, as *cylindrical* or *terete*, *quadrangular* or *square*, *jointed* or *articulated*, etc. The following are some of the more important modifications of stems: The crown of the root is a shortened stem, often partially underground, which remains in some plants after the leaves, branches and flower-stalks have withered. In this case the internodes are very short, and the nodes are crowded together, so that the plant appears to be stemless. It is seen in perennial plants, the leaves of which die down to the ground annually. A *rhizome* or *rootstock* is a horizontal stem

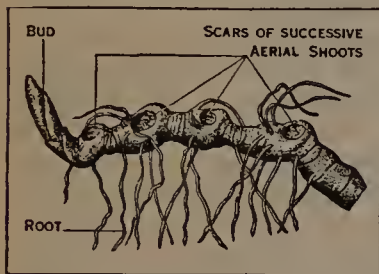


FIG. 8.—RHIZOME OF *POLYGONATUM MULTIFLORUM*

usually sending out numerous roots and leaf-buds from its upper surface. It occurs in ferns, iris, *Hedychium*, *Acorus* or sweet flag, ginger, waterlily, many species of *Carex*, rushes, anemone, etc. The leaves are reduced to scales and by their presence, the absence of a root-cap and the presence of a bud at the apex, a rhizome can be distinguished from a root.

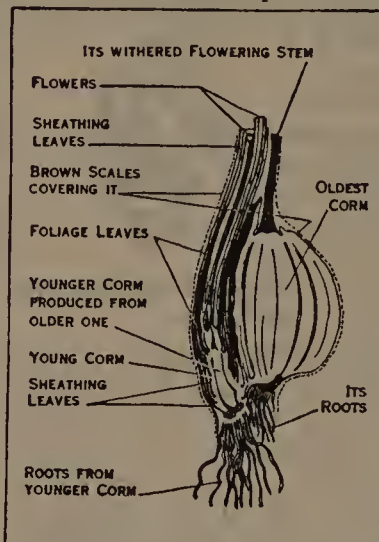


FIG. 9.—CORM OF MEADOW SAFFRON

A rhizome such as occurs in Solomon's seal is not a single stem, i.e., the product of a single bud, but is composed of portions of successive axes, the aerial parts of which have died off, leaving their scars. A rhizome sometimes assumes an erect form, as in *Scabiosa succisa*, in which the so-called *praemorse* root is in reality a rhizome, with the lower end decaying. The erect rhizome of *Cicuta virosa* (water-hemlock) shows hollow internodes, separated by partitions. In the coral-root orchid *Corallorhiza*, which grows in soil rich in humus, no roots at all are developed, the coral-like branching rhizome acting as the absorbing organ. A *tuber* is a thickened stem or branch produced by the reduction of the distance between the nodes and the swelling of the internodes, as in the potato. The eyes of the potato are leaf-buds. Tubers are sometimes aerial, occupying the place of branches. The ordinary herbaceous stem of the potato, when cut into slips and planted, sends off branches from its base, which assume the form of tubers. Tubers frequently store up a quantity of starch, as in *Maranta arundinacea*, whence West Indian arrow-root is derived.

Another form of thickened underground stem is the *corm*, as seen in the autumn crocus (*Colchicum*), gladiolus, etc. Structurally it is composed of a solid more or less rounded axis covered by a layer of thin membranous scales. A corm is only of one year's duration, giving off buds annually in the form of young corms. In autumn the young corm gives origin to leaves, the lower of which form sheaths round the corm and flower stalk, the upper

remaining very small; and in the axil of the uppermost leaves the flowering-stem develops and bears the flowers. Meanwhile in the axil of one of the middle leaves on the corm, a bud—the rudiment of a new corm—appears. The flowering-stem dies down, and the young corm from which it arose enlarges greatly during the winter at the expense of its parent corm, which thus becomes shrivelled. In spring the leaves produced on it, which were merely rudiments



FROM SACHS, "TEXT BOOK OF BOTANY" (CLARENDON PRESS)

FIG. 10.—CORMS OF *COLCHICUM AUTUMNALE*

in autumn, appear above ground as conspicuous large leaves. At the end of spring these leaves die down, the bases of the lower ones alone remaining, and constituting thin brown scales around the corm. Meanwhile, the young bud-corm in the axil of the middle leaf grows rapidly at the expense of its parent corm, but it does not attain a great size. In autumn it produces new leaves, which remain small, but from the axil of the two upper the flowering stem rises up and bears flowers; whilst in the axil of one of its middle leaves a new bud-corm appears, which will the following autumn produce young leaves, flowering stem, and a new bud-corm, and thus the cycle goes on.

The *bulb* is another form of underground stem or bud. The axis in this case is much shortened, and the internodes are hardly developed. The bases of the leaves rising from the stem are quite close together, and become succulent and enclose the axis. In the lily the thick and narrow scales are arranged separately in rows, and the bulb is called *scaly*; while in the leek, onion and tulip the scales are broad, and enclose each other in a concentric manner, the outer ones being thin and membranous, and the bulb is *tunicated*. In the axils of these fleshy scales new lateral shoots arise, forming new bulbs. The lateral buds sometimes remain attached to the axis, and produce flowering stems, so that apparently the same bulb continues to flower for many years, as in the hyacinth and tulip; at other times the young bulbs are detached, and form separate plants.

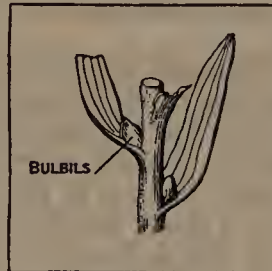


FIG. 11.—STEM OF BULBIFEROUS LILY

In the axil of the leaves of *Lilium bulbiferum*, *Dentaria bulbifera*, and some other plants, small conical or rounded bodies are produced, called *bulbils* or *bulblets*. They resemble bulbs in their



FIG. 12.—LEAF OF *BRYOPHYLLUM CALYCINUM*

aspect, and consist of a small number of thickened scales enclosing a growing-point. These scales are frequently united closely together, so as to form a solid mass. The scales in bulbs vary in number. In *Gagea* there is only one scale; in the tulip and *Fritillaria imperialis* they vary from two to five; while in lilies and hyacinths there are a great number of scales.

**Adventitious Shoots.**—Adventitious shoots are those which arise elsewhere than in the normal predetermined place, as from old stems or roots. Such shoots are frequent on the roots of elm, poplar, plum and other fruit-trees. Occasionally adventitious buds are produced on the edges of leaves, as in *Bryophyllum calycinum*, *Malaxis paludosa*, and various species of *Asplenium*, and on the surface of leaves, as in *Ornithogalum thyrsoides*. These are capable of forming independent plants. Similar buds are also made to appear on the leaves of *Begonia*, *Gesnera*, *Gloxinia* and *Achimenes*, by wounding various parts of them, and placing them in moist soil; a method pursued by gardeners in their propagation.





1. Section and whole fruit of ash. 2. Strawberry. 3. Fruit of Rose. 4. Fig fruit. 5. Cherry. 6. Seed-vessel of Camplion. 7. Poppy capsule. 8. Pea pod. 9 and 10. Meadow Saffron capsules and seeds. 11. Diagram of pentalocular capsule. 12. Flower-de-Luce capsule. 13. Diagram showing loculicidal dehiscence. 14. Diagram showing septifragal dehiscence. 15. Seed-vessel of Wall-flower. 16. Orchid capsule. 17. Seed-vessel of Anagallis arvensis. 18. Lomentum of Hedysarum. 19. Geranium fruit. 20. Dry one-seeded Dock fruit. 21. Achene of Ranunculus arvensis. 22. Samara of maple. 23. Section of wheat-grain. 24. Comfrey fruit. 25. Ovary of Foeniculum officinale. 26 a and b. Carum Carui fruit. 27. Quercus Aegilops, acorn. 28. Columbine fruit. 29. Single follicle. 30. Section of Gooseberry. 31. Section of Apple. 32. Section of Melon. 33. Honesty, septum of fruit. 34. Silicula of Shepherd's purse. 35. Asclepias seed



**ANNUALS**, in botany, the name applied to plants which complete their life-cycle in one year, in contradistinction to biennials (*q.v.*), which require two years and perennials (*q.v.*), which live for an indefinite number of years.

**FRUIT**, in its popular sense is any product of the soil that can be enjoyed by man or animals; in the Bible the word is often extended to include the offspring of man and of animals, *e.g.*, in such expressions as "the fruit of the womb," "fruit of thy cattle" (Deut. xxviii. 4). More often it is employed to denote a group of edible parts of plants, as contrasted with another group termed "vegetable." But the term is a loose one, including, *e.g.*, the stalks of the rhubarb.

In its strict botanical sense the fruit is developed from the flower as a result of fertilization of the ovule. This phenomenon induces various changes: the anther and stigma wither, the petals drop off and the sepals may be shed or undergo modifications; the ovary enlarges to form the *pericarp* and the ovules develop into the seeds, containing the embryo-plant. The term fruit is strictly applied only to the mature pistil or ovary, but it often includes other parts of the flower. Normally no fruit is produced unless fertilization is effected; but in certain plants, mostly cultivated varieties, this is not the case (*e.g.*, the seedless oranges and grapes, the banana and the bread-fruit).

**Functions of Fruit.**—The fruit protects the growing and aids in distributing the mature seeds. This latter function is very important and numerous devices secure a wide and effective dispersal. These may be classified according to the agents employed as animate and inanimate. To the second group belong also those methods by which the plant itself propels the seed forcibly from the fruit. Some plants employ a combination of the two. Thus in the gorse the seeds are shot out by the splitting and curling of the pod in which they are contained, and they must then be buried by ants in order to germinate. Violent dehiscence occurs in many plants (fig. 28). In the squirting cucumber the walls of the pericarp exert pressure on the pulpy contents in which the seeds are placed. In the balsam (*Impatiens*) also the seeds are actively expelled. Other inanimate agents are water and wind. Fruits or seeds are sometimes sufficiently buoyant to float for a long time in water. Thus the coconut may be carried hundreds of miles in the sea; the fruits and seeds of West Indian plants are sometimes thrown up by the Gulf Stream on the coasts of Europe and will often germinate; in the water lily and many other aquatic plants, the seeds float for a time before sinking to the bottom. In many cases the wind plays a part in distribution. In the poppy and many Caryophyllaceae (figs. 6, 7) there is a capsule opening by pores borne on a long stalk which sways in the wind, thus jerking out the seeds. In the pine, sycamore (fig. 22), ash (fig. 1) and many others, there is a wing-like development; in numerous Compositae the fruit is crowned by a plumose pappus (*e.g.*, dandelion, thistle); in the clematis, the style becomes feathery, while the seeds of the willow and poplar bear tufts of silky hairs. The fruit of the bladder-senna (*Colutea*) is easily rolled by the wind, while in the Rose of Jericho (*Anastatica hierochuntina*), the whole plant dries up after developing its fruits and forms a mass, easily rolled over the dry ground by the wind.

Birds and mammals are also utilized as dispersal agents by plants. The mistletoe develops a sticky layer round the seeds which stick to the bill of the bird that eats the berries; these may be wiped off on the bark of trees, thus transporting the embryo to a new host. More commonly, the fruit develops hooks which become entangled in the fur or feathers. Such are the fruits of cleavers (*Galium aparine*), *Ranunculus arvensis* (fig. 21), etc. Another method is to provide the seed with a hard covering, while surrounding this with a succulent and often brightly coloured integument; thus the seed can pass through the alimentary tract of an animal without injury, *e.g.*, plum, cherry (fig. 5); or providing the true fruit with stiff hairs, which cling to the beak of the bird which eats the fleshy receptacle, *e.g.*, rose (fig. 3).

**Classification and Structure.**—Fruits may be divided into two groups. "A" consists of true fruits, developed from the ovary alone. Of these (1) consists of those in which the surrounding

*pericarp*, round the seed, is not fleshy or fibrous. These again may be subdivided, (i) Indehiscent fruits, not opening to allow the escape of the seeds. Such are generally one-seeded. The *achene* has the pericarp closely applied to the seeds, though separable from it. Achenes are borne singly in the dock; aggregated together in the buttercup (fig. 21); on a fleshy receptacle, which may be convex as in the strawberry (fig. 2) or concave, as in the rose (fig. 3). Thus what is popularly called the fruit of these last three is really the swollen receptacle with the carpels. In *Clematis* the style, and many *Compositae* (in which the fruit is often called a *cypsela*) the modified calyx remains adherent to the fruit. A *caryopsis* differs from an achene in that the pericarp and seed become fused; wheat and grasses generally show this type of fruit. A *nut* possesses a hardened pericarp, often surrounded by bracts at the base, and containing, when mature, a single seed. Examples are the hazelnut and the acorn (fig. 27). Achenes, in which the pericarp is extended to form a winged appendage, as in the ash (fig. 1) and sycamore (fig. 22) are often called *samaras*. Those fruits which break into two or more one-seeded, indehiscent portions (*mericarps*) are termed *schizocarps*. Examples are found in the Geraniaceae, in which the mericarps separate from below upwards, in the Euphorbiaceae, etc. (ii) Dehiscent fruits, in which the pericarp splits to allow the escape of the seeds. They are generally many-seeded. When such a fruit dehisces by the ventral or, occasionally (*Magnolia*) by the dorsal, suture, it is called a *follicle*. There are usually several aggregated together; *e.g.*, columbine (figs. 28, 29). A *legume* or *pod* differs in dehiscing by both sutures. This is characteristic of leguminous plants, such as the pea (fig. 8). In *Arachis* the fruit does not dehisce, being produced under-ground. *Hedysarum* and others have a pod that separates transversely into single-seeded mericarps (fig. 18); such a structure is called a *lomomentum* and must be looked upon as a modified legume which no longer dehisces. In *Erythrina monosperma* there is only one seed. In the Cruciferae (wallflower, cabbage, shepherd's purse), the characteristic fruit is a *siliqua* (fig. 34), which is long and narrow, or short and broad, *silicula*. In both of these there are two carpels, dehiscing by two valves from below upwards, the valves separating from the placentas and leaving them united by a false septum. As in the legume, single-seeded and lomentalceous modifications are found. It is a development of the type of fruit known as a *capsule*, which is exhibited by the iris (fig. 12). Capsules which open by pores (*porose*) are seen in the poppy (fig. 7) and *Campanula*. A *pyxidium* is a capsule opening by a lid, as in the pimpernel (fig. 17). Another type of capsule is exhibited by the Geraniaceae (fig. 19). (2) Fruits in which the pericarp is differentiated into distinct layers, one of which is succulent or fibrous. To this group belong many of the edible fruits. In the *drupe*, as shown by the cherry (fig. 5), plum, etc., the endocarp is usually hard and the mesocarp pulpy and succulent, though in the almond it is tough and in the coconut fibrous. In the raspberry and bramble several small drupes are aggregated into an *etaerio*. The *berry* includes various types of fruit, all characterized by the fact that the seeds are immersed in pulp. To this group belong the barberry, gooseberry (fig. 30), currant and pomegranate.

"B."—Fruits which include parts other than the ovary. These are called *pseudocarps* or false fruits. The fleshy, indehiscent *pome* of the apple (fig. 31), hawthorn, etc., incorporates the receptacle, which becomes much swollen. The true fruit is the core. Superficially the pome resembles the "hip" of the rose. The fruits of the pineapple (*sorosis*) and fig (fig. 4) are compound pseudocarps, *i.e.*, are formed from a number of flowers. In the pineapple, the fruit called a *sorus* is formed by the coalescence of a spike of flowers, as is also the case in the mulberry. In the fig, the whole inflorescence is a hollow structure bearing male and female flowers in the cavity; each female flower forms a single true fruit. (See ANGIOSPERMS; FLOWER; SEED.)

**GRAIN**, the seed, or "fruit," of cereals, and hence cereal plants generally (from Lat. *granum*, seed).

**DURAMEN**, a botanical term for the inner, harder wood of a tree, the heart-wood.



**THORN**, in botany, a hard pointed structure, also termed a "spine," generally representing a small branch, as in hawthorn, where a normal branch arising in the axil of a leaf is replaced by a sharply pointed thorn; accessory buds on each side of the thorn and developed in the same leaf-axil will grow in the next season into ordinary branches. The similarly developed thorns of the honey-locust (*Gleditschia*) are branched. In other cases, as the sloe or the wild pear, branches become spiny at the apex tapering into a stiff leafless point. On a cultivated tree these branches disappear owing to their more vigorous growth. Leaves may be modified into spines, as in barberry, the leaves of which show every gradation between a leaf with a spiny-toothed edge and those which have been reduced to simple or multiple spines. In some species of *Astragalus* the petiole of the pinnately compound leaf persists after the fall of the leaflets as a sharp spine. In the false acacia (*Robinia*) the stipules are represented by spines.

**HERB**, in botany, the name given to those plants whose stem or stalk dies entirely or down to the root each year, and does not become, as in shrubs or trees, woody or permanent; such plants are also called "herbaceous." The term "herb" is also used of those herbaceous plants, which possess certain properties, and are used for medicinal purposes, for flavouring or garnishing in cooking, and also for perfumes (see HORTICULTURE).

**GROWTH** may be defined as increase in volume or in bulk, and as such it may apply to anything, alive or dead. The most important use of the term is that which concerns the growth of living organisms, or organic growth, for growth is one of the fundamental properties of life.

**Growth in Plants.**—It is a peculiarity of the higher plants (trees, shrubs, etc.) that they grow actively throughout life, although this growth may in other than tropical climates be restricted to certain seasons. The apex of the stem is called the growing-point, and it is made up of a number of small, simple cells, capable of rapid multiplication. The simplicity of such cells is expressed by calling them embryonic or undifferentiated, and this condition is to be contrasted with that of older cells which are more complicated in structure (differentiated) and less easily capable of growth. New cells are thus continuously being produced and left behind by the growing-point as it moves further up. The material of which the new cells are composed is derived from the building up of new living matter or protoplasm out of food. The chief factor in the upward growth of the stem of a plant, however, is the absorption of water by the cells at some little distance beneath the growing-point. The result of this process is that the cells become distended and elongated, and it illustrates the fact that growth may be due to the inflating effect of non-living substances (such as water), as well as to the production of new living matter. The apex of the root is provided with a growing-point analogous to that of the stem, differing in that it is protected by a cap of cells which prevents the growing-point itself from being injured in its downgrowth through the soil. The root similarly elongates by the absorption of water by the cells.

In addition to growing in length, the stems and roots of dicotyledons and gymnosperms are capable of another kind of growth, which results in the increase of their diameter. This is brought about by the formation of a cylindrical zone of embryonic cells, called the cambium, which, as its cells divide, produces new bast on the outside and new wood on the inside. In climates outside the tropics, this growth is seasonal, which accounts for the growth-rings characteristic of cross-sections of stems.

Abnormal growths in plants are to be found in the case of galls, which are developed in response to the irritation caused by certain kinds of insects in the process of depositing their eggs, and in the development of these eggs. . . . (G. R. DE B.)

**PUBLISHERS' NOTE:**—Following the *Britannica* custom, we have retained, at the end of signed articles, the initials and not the full name of the author. The reader, however, can always identify the author by referring to the List of Contributors where the full names of the authors are given together with their initials.

**LEAF**, the name given in popular language to all the green expanded organs borne upon an axis, and so applied to similar ob-

jects. Investigation has shown that many other parts of a plant which externally appear very different from ordinary leaves are, in their essential particulars, very similar to them, and are in fact their morphological equivalents. Such are the scales of a bulb, and the various parts of the flower, and assuming that the structure ordinarily termed a leaf is the typical form, these other structures were designated changed or metamorphosed leaves, a somewhat misleading interpretation.

Leaves are produced as lateral outgrowths of the stem in definite succession below the apex. This character, common to all leaves, distinguishes them from other organs. In the higher plants we can easily recognize the distinction between stem and leaf. Amongst the lower plants, however, it is found that a demarcation into stem and leaf is impossible, but that there is a structure which partakes of the characters of both—i.e., the *thallus*. The leaves always arise from the outer portion of the primary meristem of the plant, and the tissues of the leaf are continuous with those of the stem. Every leaf originates as a simple, cellular papilla, which consists of a development from the cortical layers covered by epidermis; and as growth proceeds, the fibro-vascular bundles of the stem are continued outwards, and finally expand and terminate in the leaf. The increase in length of the leaf by growth at the apex is usually of a limited nature. In some ferns, however, there seems to be a provision for indefinite terminal growth, while in others this growth is periodically interrupted. It not unfrequently happens, especially amongst Monocotyledons, that after growth at the apex has ceased, it is continued at the base of the leaf, and in this way the length may be much increased. Amongst Dicotyledons this is very rare. In all cases the dimensions of the leaf are enlarged by interstitial growth of its parts.

**Structure of Leaves.**—The simplest leaf is found in some mosses, where it consists of a single layer of cells. The typical foliage leaf consists of several layers, and amongst vascular plants is distinguishable into an outer layer (*epidermis*) and a central tissue (*mesophyll*) with fibro-vascular bundles distributed through it. (See PLANTS: *Anatomy*.)

The form and arrangement of the parts of a typical foliage leaf are intimately associated with the part played by the leaf in the life of the plant. The flat surface is spread to allow the maximum amount of sunlight to fall upon it, as it is by the absorption of energy from the sun's rays by means of the chlorophyll contained in the cells of the leaf that the building up of plant food is rendered possible; this process is known as photosynthetic assimilation of carbon dioxide or simply photosynthesis. The first stage is the combination of carbon dioxide, absorbed from the air taken in through the stomata into the living cells of the leaf, with water which is brought into the leaf by the wood-vessels. The wood-vessels form part of the fibro-vascular bundles or veins of the leaf and are continuous throughout the leaf-stalk and stem with the root by which water is absorbed from the soil. The palisade layers of the mesophyll contain the larger number of chlorophyll grains (or chloroplasts) while the absorption of carbon dioxide is carried on chiefly through the lower epidermis which is generally much richer in stomata. The water taken up by the root from the soil contains nitrogenous and mineral salts which combine with the first product of photosynthesis—a carbohydrate—to form more complicated nitrogen-containing food substances of a protein nature; these or their simpler products are then distributed by other elements of the vascular bundles (the phloem) through the leaf to the stem and so throughout the plant to wherever growth or development is going on. A large proportion of the water which ascends to the leaf passes out in the form of water vapour through the stomata—this process is known as transpiration. Hence the extended surface of the leaf exposing a large area to light and air is eminently adapted for the carrying out of the process of photosynthesis and transpiration. The arrangement of the leaves on the stem and branches (see *Phyllotaxis*, below) is such as to prevent the upper leaves' shading the lower, and the shape of the leaf serves towards the same end—the disposition of leaves on a branch or stem is often seen to form a "mosaic," each leaf fitting into the space between neighbouring leaves and the branch on which they are borne without overlapping.



Submerged leaves, or leaves which are developed under water, differ in structure from aerial leaves. They have usually no fibro-vascular system, but consist of a congeries of cells, which sometimes become elongated and compressed so as to resemble veins. They have a layer of compact cells on their surface, but no true epidermis, and no stomata. Their internal structure consists of cells, disposed irregularly, and sometimes having spaces which are filled with air for the purpose of floating the leaf. When exposed to the air these leaves easily part with their moisture, and become shrivelled and dry. In some cases there is only a network of filament-like cells, the spaces between which are not filled with parenchyma, giving a skeleton appearance to the leaf, as in *Ouvirandra fenestralis* (Lattice plant).

#### GROSS ANATOMY

A leaf, whether aerial or submerged, generally consists of a flat expanded portion, called the blade, or *lamina*, of a narrower portion called the *petiole* or stalk, and sometimes of a portion at the base of the petiole, which forms a sheath or *vagina*, or is developed in the form of outgrowths, called *stipules*. All these portions are not always present. The sheathing or stipulary portion is frequently wanting. When a leaf has a distinct stalk it is *petiolate*; when it has none, it is *sessile*, and if in this case it embraces the stem it is said to be *amplexicaul*. The part of the leaf next the petiole or the axis is the *base*, while the opposite extremity is the *apex*. The leaf is usually flattened and expanded horizontally, *i.e.*, at right angles to the longitudinal axis of the shoot, so that the upper face is directed towards the heavens, or the lower towards the earth. In some cases leaves, as in *Iris*, or leaf-like petioles, as in Australian species of *Acacia* and *Eucalyptus*, have their plane of expansion parallel to the axis of the shoot, there is then no distinction into an upper and a lower face, but the two sides are developed alike; or the leaf may have a cylindrical or polyhedral form, as in *mesembryanthemum*. The upper angle formed between the leaf and the stem is called its *axil*; it is there that leaf-buds are normally developed. The leaf is sometimes articulated with the stem, and when it falls off a *scar* remains; at other times it is continuous with it, and then decays, while still attached to the axis. In their early state all leaves are continuous with the stem, and it is only in their after growth that articulations are formed. When leaves fall off annually they are called *deciduous*; when they remain for two or more years they are *persistent*, and the plant is *evergreen*. The laminar portion of a leaf is occasionally articulated with the petiole, as in the orange, and a joint at times exists between the vaginal or stipulary portion and the petiole.

**Venation.**—The arrangement of the fibro-vascular system in the lamina constitutes the *venation*. In an ordinary leaf, as that of the elm, there is observed a large central vein running from the base to the apex of the leaf, this is the *midrib* (fig. 1); it gives off veins laterally (*primary veins*). The venation is described as pinnate or feather-veined. In some cases, as sycamore or castor oil (fig. 2), in place of there being only a single midrib there are several large veins (*ribs*) of nearly equal size, which diverge from the point where the blade joins the petiole or stem, giving off lateral veins. The venation is then palmate. The primary veins give off secondary veins, and these in their turn give off tertiary veins, and so on until a complete network of vessels is produced, and those veins usually project on the under surface of the leaf. To a distribution of veins such as this the name of *reticulated* or *netted* venation has been applied. In the leaves of some plants there exists a midrib with large veins running nearly parallel to it from the base to the apex of the lamina, as in grasses (fig. 3); or with veins diverging from the base of the lamina in more or less parallel lines, as in fan palms (fig. 7), or with veins coming off from it throughout its whole course, and running parallel to each other in a straight or curved direction towards the margin of the leaf, as in plantain and banana. In these cases the veins are often united by cross veinlets, which do not, however, form an angular network. Such leaves are said to be *parallel-veined*. The leaves of Monocotyledons have generally this kind of venation, while reticulated venation most usually occurs amongst Dicotyledons.

Some plants, which in most points of their structure are monocotyledonous, yet have reticulated venation; as in *Smilax* and *Dioscorea*. The distribution of the system of vessels in the leaf is usually easily traced, but in the case of succulent plants, as *Hoya*, agave, stonecrop and *mesembryanthemum*, the veins are obscure. The function of the veins, which consist of vessels and fibres, is to form a rigid framework for the leaf and to conduct liquids.

In nearly all plants, except Thallophyta, leaves are present at some period of their existence. In *Cuscuta* (Dodder) (*q.v.*), however, we have an exception. The forms assumed by leaves vary much, not only in different plants, but in the same plant. It is only amongst the lower classes of plants—Mosses, Characeae, etc.—that all the leaves on a plant are similar. As we pass up the scale of plant life we find them becoming more and more variable. The structures in ordinary language designated as leaves are considered so *par excellence*, and they are frequently spoken of as *foliage leaves*. In relation to their production on the stem we may observe that when they are small they are always produced in great number, and as they increase in size their number diminishes correspondingly. The cellular process from the axis which develops into a leaf is simple and undivided; it rarely remains so, but in progress of growth becomes segmented in various ways, either longitudinally or laterally, or in both ways. By longitudinal segmentation we have a leaf formed consisting of sheath, stalk and blade; or one or other of these may be absent, and thus stalked, sessile, sheathing, etc., leaves are produced. Lateral segmentation affects the lamina, producing indentations, lobings or fissuring of its margins. In this way two marked forms of leaf are produced—(1) *Simple* form, in which the segmentation, however deeply it extends into the lamina, does not separate portions of the lamina which become articulated with the midrib or petiole; and (2) *Compound* form, where portions of the lamina are separated as detached *leaflets*, which become articulated with the midrib or petiole. Of both simple and compound leaves, according to the amount of segmentation and the mode of development of the parenchyma and direction of the fibro-vascular bundles, many forms are produced.

**Simple Leaves.**—When the parenchyma is developed symmetrically on each side of the midrib or stalk, the leaf is *equal*; if otherwise, the leaf is *unequal* or *oblique* (fig. 1). If the margins are even and present no divisions, the leaf is *entire*; if there are slight projections which are more or less pointed, the leaf is *dentate* or toothed; when the projections lie regularly over each other, like the teeth of a saw, the leaf is *serrate* (fig. 1); when they are rounded the leaf is *crenate*. If the divisions extend more deeply into the lamina than the margin, the leaf receives different names according to the nature of the segments; thus, when the divisions extend about half-way down (fig. 4), it is *cleft*; when the divisions extend nearly to the base or to the midrib the leaf is *partite*.

If these divisions take place in a simple *feather-veined* leaf it becomes either *pinnatifid* (fig. 4), when the segments extend to about the middle, or *pinnatipartite*, when the divisions extend nearly to the midrib. These primary divisions may be again subdivided in a similar manner, and thus a feather-veined leaf will become *bipinnatifid* or *bipinnatipartite*; still further subdivisions give origin to *tripinnatifid* and *lacinated* leaves. The same kinds of division taking place in a simple leaf with palmate or *radiating* venation, give origin to *lobed*, *cleft* and *partite* forms. The name *palmate* or *palmatifid* (fig. 2) is the general term applied to leaves with radiating venation, in which there are several lobes united by a broad expansion of parenchyma, like the palm of the hand, as in the sycamore, castor-oil plant, etc. The divisions of leaves with radiating venation may extend to near the base of the leaf, and the names *bipartite*, *tripartite*, *quinquepartite*, etc., are given according as the partitions are two, three, five or more. The term *dissected* is applied to leaves with radiating venation, having numerous narrow divisions, as in *Geranium dissectum*.

When in a radiating leaf there are three primary partitions, and the two lateral lobes are again cleft, as in hellebore, the leaf is called *pedate* or *pedatifid*, from a fancied resemblance to the claw of a bird. In all the instances already alluded to the leaves have been considered as flat expansions, in which the ribs or veins





1. Leaf of elm (*Ulmus*). 2. Palmately cleft leaf of castor-oil plant (*Ricinus communis*). 3. Stem of a grass *Poa* with leaf. 4. Runcinate leaf of dandelion. 5. Five-partite leaf of aconite. 6. Peltate leaves of Indian cress (*Tropaeolum majus*). 7. Lanceolate leaf of species of senna. 8. Oblong leaf of species of senna. 9. Emarginate leaf of species of senna. 10. Reniform leaf (*Nepeta glechoma*), margin crenate. 11. Sagittate leaf of *Convolvulus*. 12. Palmately compound leaf of Horse-chestnut (*Aesculus hippocastanum*). 13. Imparipinnate (unequally pinnate) leaf of Robinia. 14. Branch and leaves of sensitive plant (*Mimosa pudica*). 15. Leaf of an acacia (*Acacia heterophylla*). 16. Leaf of pansy, showing stipules. 17. Stem with opposite leaves. 18. Stem with alternate leaves, arranged in pentastichous or quincuncial manner. 19. Portion of a branch of a lime tree (*Tilia*). 20. Part of branch cherry with six leaves. (A) branch, with leaves numbered in order; (B) magnified representation of branch, showing points of insertion of leaves and their spiral arrangement. 21. Diagram of a phyllotaxis represented by the fraction  $\frac{2}{5}$ . 22. Circinate vernation. 23. Transverse section of conduplicate leaf. 24. Transverse section of plicate or platted leaf. 25. Transverse section of convoluted leaf. 26. Transverse section of involute leaf. 27. Transverse section of revolute leaf. 28 and 29. Transverse sections of buds in which leaves are respectively arranged in an accumbent and an equitant manner. 30. Transverse section of a bud, showing two leaves folded in an obvolvute manner. 31. Transverse section of a bud, showing two leaves arranged in a supervolute manner.

spread out on the same plane with the stalk. In some cases, however, the veins spread at right angles to the stalk, forming a *peltate* leaf as in Indian cress (fig. 6).

The form of the leaf shows a very great variety, ranging from the narrow *linear* form with parallel sides, as in grasses or the needle-like leaves of pines and firs, to more or less rounded or *orbicular*—descriptions of these will be found in works on descriptive botany—a few examples are illustrated here (figs. 8, 9, 10). The apex also varies considerably, being rounded, or *obtus*, sharp or *acute*, notched (fig. 19), etc. Similarly the shape of the base may

vary, when rounded lobes are formed, as in dog-violet, the leaf is *cordate* or heart-shaped; or kidney-shaped or *reniform* (fig. 10) when the apex is rounded as in ground ivy. When the lobes are prolonged downwards and are acute, the leaf is *sagittate* (fig. 11); when they proceed at right angles, as in *Rumex Acetosella*, the leaf is *hastate* or halbert-shaped. When a simple leaf is divided at the base into two leaf-like appendages, it is called *auriculate*. When the development of parenchyma is such that it more than fills up the spaces between the veins, the margins become *wavy*, *crisp* or *undulated*, as in *Rumex crispus* and *Rheum undulatum*. By cul-



tivation the cellular tissue is often much increased, giving rise to the *curled* leaves of greens, savoys, cresses, lettuce, etc.

**Compound Leaves.**—Compound leaves are those in which the divisions extend to the midrib or petiole, and the separated portions become each articulated with it, and receive the name of *leaflets*. The midrib, or petiole, has thus the appearance of a branch with separate leaves attached to it, but it is considered properly as one leaf, because in its earliest state it arises from the axis as a single piece, and its subsequent divisions in the form of leaflets are all in one plane. The leaflets are either sessile (fig. 12) or have stalks, called *petiolules* (fig. 13). Compound leaves are pinnate (fig. 13) or palmate (fig. 12) according to the arrangement of leaflets. When a pinnate leaf ends in a pair of pinnae it is *equally* or *abruptly pinnate* (paripinnate); when there is a single terminal leaflet (fig. 13), the leaf is *unequally pinnate* (imparipinnate); when the leaflets or pinnae are placed alternately on either side of the midrib, and not directly opposite to each other, the leaf is *alternately pinnate*; and when the pinnae are of different sizes, the leaf is *interruptedly pinnate*. When the division is carried into the second degree, and the pinnae of a compound leaf are themselves pinnately compound, a bipinnate leaf is formed.

**Petiole.**—The *petiole* or leaf-stalk is the part which unites the limb or blade of the leaf to the stem. It is absent in *sessile* leaves, and this is also frequently the case when a sheath is present, as in grasses (fig. 3). It consists of the fibro-vascular bundles with a varying amount of cellular tissue. When the vascular bundles reach the base of the lamina they separate and spread out in various ways, as already described under venation. The lower part of the petiole is often swollen (fig. 14), forming the *pulvinus*, formed of cellular tissue, the cells of which exhibit the phenomenon of irritability. In *Mimosa pudica* (fig. 14) and other species, a sensitiveness is located in the pulvinus which upon irritation induces a depression of the whole bipinnate leaf. A similar property exists in the pulvini at the base of the leaflets which fold upwards. The petiole varies in length, being usually shorter than the lamina, but sometimes much longer. In some palms it is 15 or 20 ft. long, and is so rigid as to be used for poles or walking-sticks. In general, the petiole is more or less rounded in its form, the upper surface being flattened or grooved. Sometimes it is compressed laterally, as in the aspen, and to this peculiarity the trembling of the leaves of this tree is due. At other times it is winged, as in lemon and *Dionaea*, or pitcher like, as in *Sarracenia*. In certain of the Australian acacias, and in some species of *Oxalis* and *Bupleurum*, the petiole is flattened in a vertical direction, the vascular bundles separating immediately after quitting the stem and running nearly parallel from base to apex. This kind of petiole (fig. 15) has been called a *phyllode*. In these plants the laminae or blades of the leaves are pinnate or bipinnate, and are produced at the extremities of the phyllodes in a horizontal direction; but in many instances they are not developed, and the phyllode serves the purpose of a leaf. Some petioles are long, slender and sensitive to contact, and function as tendrils by means of which the plant climbs; as in the garden nasturtiums (*Tropaeolum*), clematis and others; and in compound leaves the midrib and some of the leaflets may similarly be transformed into tendrils, as in the pea and vetch.

**Leaf Base.**—The leaf base is often developed as a *sheath* (*vagina*), which embraces the whole or part of the circumference of the stem (fig. 3). This sheath is comparatively rare in dicotyledons, but is seen in plants of the family Umbelliferae. It is much more common amongst monocotyledons. In sedges the sheath forms a complete investment of the stem, whilst in grasses it is split on one side. In the latter plants there is also a membranous outgrowth, the *ligule*, at right angles to the median plane of the leaf from the point where the sheath passes into the lamina, there being no petiole (fig. 3).

In leaves in which no sheath is produced we not infrequently find small foliar organs, *stipules*, at the base of the petiole (fig. 16). The stipules are generally two in number, and they are important as supplying characters in certain natural orders. Thus they occur in the pea and bean family, in rosaceous plants and the family Rubiaceae. They are not common in dicotyledons with

opposite leaves. Plants having stipules are called *stipulate*; those having none are *exstipulate*. Stipules may be large or small, entire or divided, deciduous or persistent. They are not usually of the same form as the ordinary foliage leaves of the plant, from which they are distinguished by their lateral position at the base of the petiole. In the pansy (fig. 16) the true leaves are stalked and crenate, while the stipules are large, sessile and pinnatifid. In *Lathyrus Aphaca* and some other plants the true pinnate leaves are abortive, the petiole forms a tendril, and the stipules alone are developed, performing the office of leaves. In other instances the stipules unite together on the side of the stem opposite the leaf forming an *ochrea*, as in the dock family. The stipules are sometimes so minute as to be scarcely distinguishable without the aid of a lens, and so fugacious as to be visible only in the very young state of the leaf. They may assume a hard and spiny character, as in *Robinia Pseudacacia* (fig. 13), or, as in *Smilax*, each stipule may be represented by a tendril. At the base of the leaflets of a compound leaf, small stipules (*stipels*) are occasionally produced.

**Modifications.**—Variations in the structure and forms of leaves and leaf-stalks are produced by the increased development of cellular tissue, by the abortion or degeneration of parts, by the multiplication or repetition of parts and by adhesion. When cellular tissue is developed to a great extent, leaves become succulent and occasionally assume a crisp or curled appearance. Such changes take place naturally, but they are often increased by the art of the gardener, and the object of many horticultural operations is to increase the bulk and succulence of leaves. It is in this way that cabbages and savoys are rendered more delicate and nutritious. The leaves of barberry and of some species of *Astragalus*, and the stipules of the false acacia (*Robinia*) are spiny. To the same cause is due the spiny margin of the holly-leaf. When two lobes at the base of a leaf are prolonged beyond the stem and unite, the leaf is *perfoliate*, the stem appearing to pass through it, as in *Bupleurum perfoliatum* and *Chlora perfoliata*; when two leaves unite by their bases they become *connate*, as in *Lonicera Caprifolium*; and when leaves adhere to the stem, forming a sort of winged or leafy appendage, they are *decurrent*, as in thistles. The formation of peltate leaves has been traced to the union of the lobes of a cleft leaf. In the leaf of the *Victoria regia* the transformation may be traced during germination. The first leaves produced by the young plant are linear, the second are sagittate and hastate, the third are rounded-cordate and the next are orbicular. The cleft indicating the union of the lobes remains in the large leaves. The parts of the leaf are frequently transformed into *tendrils*, with the view of enabling the plants to twine round others for support. In Leguminous plants (the pea tribe) the pinnae are frequently modified to form tendrils, as in *Lathyrus Aphaca*, in which the stipules perform the function of true leaves. In *Flagellaria indica*, *Gloriosa superba* and others, the midrib of the leaf ends in a tendril. In *Smilax* there are two stipular tendrils.

The pitchers of insectivorous plants are formed either by petioles or by laminae, and they are composed of one or more leaves. In *Sarracenia* and *Heliamphora* the pitcher is composed of the petiole of the leaf. In *Nepenthes* the pitcher is a modification of the lamina, the petiole often plays the part of a tendril, while the leaf base is flat and leaf-like.

In *Utricularia* bladder-like sacs are formed by a modification of leaflets on the submerged leaves.

In some cases the leaves are reduced to mere *scales*—*cataphyllary* leaves; they are produced abundantly upon underground shoots. In parasites (*Lathraea*, *Orobanche*) and in plants growing on decaying vegetable matter (*saprophytes*), in which no chlorophyll is formed, these scales are the only leaves produced. In *Pinus* the only leaves produced on the main stem and the lateral shoots are scales, the acicular leaves of the tree growing from axillary shoots. In *Cycas* whorls of scales alternate with large pinnate leaves. In many plants, as already noticed, phyllodes or stipules perform the function of leaves. The production of leaf-buds from leaves sometimes occurs as in *Bryophyllum*, and many plants of the order Gesneraceae. The leaf of Venus's fly-trap



(*Dionaea muscipula*) when cut off and placed in damp moss, with a pan of water underneath and a bell-glass for a cover, has produced buds from which young plants were obtained. Some species of saxifrage and of ferns also produce buds on their leaves and fronds. In *Nymphaea micrantha* buds appear at the upper part of the petiole.

**Phyllotaxis.**—Leaves occupy various positions on the stem and branches, and have received different names according to their situation. Thus leaves arising from the crown of the root, as in the primrose, are called *radical*; those on the stem are *cauline*; on flower-stalks, *floral* leaves (see FLOWER). The first leaves developed are known as seed leaves or *cotyledons*. The arrangement of the leaves on the axis and its appendages is called *phyllotaxis*.

In their arrangement leaves follow a definite order. The points on the stem at which leaves appear are called *nodes*; the part of the stem between two nodes is the *internode*. When two leaves are produced at the same node, one on each side of the stem or axis, and at the same level, they are *opposite* (fig. 18); when more than two are produced they are *verticillate*, and the circle of leaves is then called a *verticil* or *whorl*. When leaves are opposite, each successive pair may be placed at right angles to the pair immediately preceding. They are then said to *decussate*, following thus a law of alternation (fig. 17). The same occurs in the verticillate arrangement, the leaves of each whorl rarely being *superposed* on those of the whorl next it, but usually alternating so that each leaf in a whorl occupies the space between two leaves of the whorl next to it. There are considerable irregularities, however, in this respect, and the number of leaves in different whorls is not always uniform, as may be seen in *Lysimachia vulgaris*. When a single leaf is produced at a node, and the nodes are separated so that each leaf is placed at a different height on the stem, the leaves are *alternate* (fig. 18). A plane passing through the point of insertion of the leaf in the node, dividing the leaf into similar halves, is the median plane of the leaf; and when the leaves are arranged alternately on an axis so that their median planes coincide they form a straight row or *orthostichy*. On every axis there are usually two or more orthostichies. In fig. 19 the leaves arise from nodes and the nodes are separated from each other by internodes, the arrangement resulting in one leaf being placed above the other. In this case, then, there are two orthostichies, and the arrangement is said to be *distichous*. When the fourth leaf is directly above the first, the arrangement is *tristichous*. The same arrangement continues throughout the branch, so that in the latter case the 7th leaf is above the 4th, the 10th above the 7th; also the 5th above the 2nd, the 6th above the 3rd and so on. The size of the angle between the median planes of two consecutive leaves in an alternate arrangement is their *divergence*; and it is expressed in fractions of the circumference of the axis which is supposed to be a circle. In a regularly-formed straight branch covered with leaves, if a thread is passed from one to the other, turning always in the same direction, a spiral is described, and a certain number of leaves and of complete turns occur before reaching the leaf directly above that from which the enumeration commenced. If this arrangement is expressed by a fraction, the numerator of which indicates the number of turns, and the denominator the number of internodes in the spiral cycle, the fraction will be found to represent the angle of divergence of the consecutive leaves on the axis. Thus, in fig. 20 *A, B*, the leaf cycle consists of five leaves, the 6th leaf being placed vertically over the 1st, the 7th over the second and so on; while the number of turns between the 1st and 6th leaf is two; hence this arrangement is indicated by the fraction  $\frac{2}{5}$ . In other words, the distance or divergence between the first and second leaf, expressed in parts of a circle, is  $\frac{2}{5}$  of a circle or  $360^\circ \times \frac{2}{5} = 144^\circ$ . In fig. 19 the spiral is  $\frac{1}{2}$ , i.e., one turn and two leaves; the third leaf being placed vertically over the first and the divergence between the first and second leaf being one-half the circumference of a circle,  $360^\circ \times \frac{1}{2} = 180^\circ$ . Again, in a tristichous arrangement the number is  $\frac{1}{3}$ , or one turn and three leaves, the angular divergence being  $120^\circ$ .

By this means we have a convenient mode of expressing on paper the exact position of the leaves upon an axis. And in many cases such a mode of expression is of excellent service in enabling us

readily to understand the relations of the leaves. The divergences may also be represented diagrammatically on a horizontal projection of the vertical axis, as in fig. 21. Here the outermost circle represents a section of that portion of the axis bearing the lowest leaf, the innermost represents the highest. The broad dark lines represent the leaves, and they are numbered according to their age and position. It will be seen at once that the leaves are arranged in orthostichies marked I–V, and that these divide the circumference into five equal portions. But the divergence between leaf 1 and leaf 2 is equal to  $\frac{2}{5}$  of the circumference, and the same is the case between 2 and 3, 3 and 4, etc. The divergence, then, is  $\frac{2}{5}$ , and from this we learn that, starting from any leaf on the axis, we must pass twice round the stem in a spiral through five leaves before reaching one directly over that with which we started. The line which, winding round an axis either to the right or to the left, passes through the points of insertion of all the leaves on the axis is termed the *genetic spiral*. In cases where the internodes are very short and the leaves are closely applied to each other, as in the house-leek, it is difficult to trace the genetic spiral.

The spiral is not always constant throughout the whole length of an axis. The angle of divergence may alter either abruptly or gradually, and the phyllotaxis thus becomes very complicated. This change may be brought about by arrest of development, by increased development of parts or by a torsion of the axis.

In dicotyledonous plants the first leaves produced (the cotyledons) are opposite. This arrangement often continues during the life of the plant, but at other times it changes, passing into distichous and spiral forms. Some tribes of plants are distinguished by the opposite or verticillate, others by their alternate, leaves. Labiate plants have decussate leaves, while Boraginaceae have alternate leaves, and Tiliaceae usually have distichous leaves; Rubiaceae have opposite leaves. Such arrangements as  $\frac{2}{5}$ ,  $\frac{3}{8}$ ,  $\frac{5}{13}$  and  $\frac{8}{21}$  are common in Dicotyledons. In monocotyledonous plants there is only one seed-leaf or cotyledon, and hence the arrangement is at first alternate; and it generally continues so more or less, rarely being verticillate. Such arrangements as  $\frac{1}{2}$ ,  $\frac{1}{3}$  and  $\frac{2}{5}$  are common in Monocotyledons, as in grasses, sedges and lilies. It has been found in general that, while the number 5 occurs in the phyllotaxis of Dicotyledons, 3 is common in that of Monocotyledons.

**Axillary Buds.**—In the axil of previously formed leaves leaf-buds arise. These leaf-buds contain the rudiments of a shoot, and consist of leaves covering a growing point. The buds of trees of temperate climates, which lie dormant during the winter, are protected by scale leaves. These scales or protective appendages of the bud consist either of the altered laminae or of the enlarged petiolar sheath, or of stipules, as in the fig and magnolia, or of one or two of these parts combined. These are often of a coarse nature, serving a temporary purpose, and then falling off when the leaf is expanded. They are frequently covered with a resinous matter, as in balsam-poplar and horse-chestnut, or by a thick downy covering as in the willow. In plants of warm climates the buds have often no protective apparatus, and are then said to be *naked*.

The arrangement of the leaves in the bud is termed *vernation* or *prefoliation*. In considering vernation we must take into account both the manner in which each individual leaf is folded and also the arrangement of the leaves in relation to each other. These vary in different plants, but in each species they follow a regular law. The leaves in the bud are either placed simply in apposition, or they are folded or rolled up longitudinally or laterally, giving rise to different kinds of vernation, as delineated in figs. 22 to 31, where the folded or curved lines represent the leaves, the thickened part being the midrib. The leaf taken individually is either folded longitudinally from apex to base, as in the tulip-tree, and called *reclinate* or *replicate*; or rolled up in a circular manner from apex to base, as in ferns (fig. 22), and called *circinate*; or folded laterally, *conduplicate* (fig. 23), as in oak; or it has several folds like a fan, *plicate* or *plaited* (fig. 24), as in vine and sycamore, and in leaves with radiating vernation, where the ribs mark the foldings; or it is rolled upon itself, *convolute* (fig. 25), as in banana and



apricot; or its edges are rolled inwards, *involute* (fig. 26), as in violet; or outwards, *revolute* (fig. 27), as in rosemary. The different divisions of a cut leaf may be folded or rolled up separately, as in ferns, while the entire leaf may have either the same or a different kind of vernation. The leaves have a definite relation to each other in the bud, being either opposite, alternate or verticillate; and thus different kinds of vernation are produced. Sometimes they are nearly in a circle at the same level, remaining flat or only slightly convex externally, and placed so as to touch each other by their edges, thus giving rise to *valvate* vernation. At other times they are at different levels, and are applied over each other, so as to be imbricated as in lilac, and in the outer scales of sycamore; and occasionally the margin of one leaf overlaps that of another, while it in its turn is overlapped by a third, so as to be *twisted*, *spiral* or *contortive*. When leaves are applied to each other face to face, without being folded or rolled together, they are *appressed*. When the leaves are more completely folded they either touch at their extremities and are *accumbent* or *opposite* (fig. 28), or are folded inwards by their margin and become *induplicate*; or a conduplicate leaf covers another similarly folded, which in turn covers a third, and thus the vernation is *equitant* (fig. 29), as in privet; or conduplicate leaves are placed so that the half of the one covers the half of another, and thus they become *half-equitant* (fig. 30), as in sage. When in the case of convolute leaves one leaf is rolled up within the other, it is *super-volute* (fig. 31). The scales of a bud sometimes exhibit one kind of vernation and the leaves another. The same modes of arrangement occur in the flower-buds.

Leaves, after performing their functions for a certain time, wither and die. In doing so they frequently change colour, and hence arise the beautiful and varied tints of the autumnal foliage. Leaves which are articulated with the stem, as in the walnut and horse-chestnut, fall and leave a scar, while those which are continuous with it remain attached for some time after they have lost their vitality. Most of the trees of Great Britain have deciduous leaves, their duration not extending over more than a few months, while in trees of warm climates the leaves often remain for two or more years. In tropical countries, however, many trees lose their leaves in the dry season. The period of defoliation varies in different countries according to the nature of the climate. Trees which are called evergreen, as pines and evergreen-oak, are always deprived of a certain number of leaves at intervals, sufficient being left, however, to preserve their green appearance. The fall is directly caused by the formation of a layer of tissue across the base of the leaf-stalk; the cells of this layer separate from one another and the leaf remains attached only by the fibres of the veins until it becomes finally detached by the wind or frost. Before its fall the leaf has become dry owing to loss of water; certain of the materials of the leaf pass back into the stem and are available for further growth. The leaf scar is protected by a change of a corky nature (suberization) in the walls of the exposed cells.

(A. B. R.; V. H. B.)

**FLORA.** The term "flora" is used in botany collectively for the plant-growth of a district.

**POLLINATION**, a term used in botany for the transference of pollen (*see* FLOWER) to the stigma (the receptive surface) of the ovary of the flower. Such pollination brings about the fertilisation of the ovules in the ovary and their subsequent development into seeds; there are, however, a few cases in which parthenogenesis occurs, *i.e.*, the ovules develop without fertilisation. As the pollen-bearing parts of the stamens are rarely in contact with the stigma at the time when both of these are ripe, some mechanism is clearly necessary to bring the pollen to the stigma. The means in question is usually wind or insects, though sometimes other agencies such as water or birds may be responsible. The great variety in the form, colour and scent of flowers has been developed in relation to the particular agency of insects. Apart from the mechanism of pollination we can distinguish two types—self-pollination (autogamy) in which pollen is transferred from the stamens of one flower to the stigma of the same flower; and cross-pollination (allogamy) in which pollen is transferred to

the stigma of another flower on the same plant (geitonogamy) or to the flower of another plant of the same species (xenogamy). Occasionally hybridization is possible, the pollen of one plant bringing about fertilisation of the ovary of the flower of another species or, more rarely, of the flower of a plant belonging to another genus; cases of hybridization between genera are known for example in cycads (*see* GYMNOSPERMS) and in orchids.

**Cross Pollination and Dichogamy.**—Cross pollination is the only possible method in the case of unisexual flowers whether the plant is *monoecious* (*i.e.*, with staminate and pistillate flowers on the same plant), as in birch, beech, elder, oak, or *dioecious* (*i.e.*, with staminate and pistillate flowers on different plants) as in the case of willows and poplars. In hermaphrodite flowers, bearing both stamens and carpels, either self-pollination or cross pollination can occur. It is interesting to note however, that many flowers have special arrangements to ensure that the pollinating mechanism, whatever it may be, causes cross pollination and not self-pollination. One of the commonest methods to achieve this is a separation *in time* of the sexes—the stamens dehisce and shed their pollen either before or after the stigma is receptive. This separation in time—and it may apply to the separate male and female flowers on the same plant—is known as *dichogamy*. When the stamens ripen first it is known as *protandry*, the more common case, while when the stigma is ready first, it is known as *proterogyny*. Protandry is very common in insect-pollinated (*entomophilous*) flowers, as in nearly all members of the Compositae (*q.v.*) and Umbelliferae, many Labiatae (such as dead-nettle [*Lamium*] and *Salvia*), the Caryophyllaceae, the large willow-herb (*Epilobium angustifolium*), etc. Proterogyny is found in the horse chestnut (*Aesculus*), the autumn crocus (*Colchicum*), many Araceae, and in wind-pollinated anemophilous flowers such as plaintain (*Plantago*), meadow rue (*Thalictrum*) and many grasses, though here separation in time is very short and many are self-pollinated as wheat, barley and oats. It is often accepted that cross-pollination is of greater value to the plant than self-pollination in respect of weight and number of seeds; the question is, however, one of some difficulty. The numerous provisions in flowers for aiding cross-pollination and hindering self-pollination suggest the superiority of the former process, but there are numerous plants which normally and for generations are self-pollinated.

#### WIND POLLINATION (ANEMOPHILY)

The method of pollination of the earlier and more primitive flowers was probably by the wind, the insect pollinated flowers being derived from them in later stages of evolution. Some flowers such as plaintain and meadow rue mentioned above, are almost certainly anemophilous by reduction, all their congeners being entomophilous; other cases are *Poterium* among the Rosaceae and Kerguelen's Land cabbage (*q.v.*) among the Cruciferae.

**Characters of Anemophilous Flowers.**—These are such as might be expected. The flowers are usually inconspicuous (the corolla being commonly absent) for there is no advantage in their being easily seen, and they are without the scent or nectar so common in flowers visited by insects. Furthermore there is usually no tubular formation of the flower and no irregularities. On the other hand these wind-pollinated flowers form large quantities of pollen, since the greater proportion when consigned to the air must necessarily be lost. The large quantity of pollen produced by pines and other conifers is well known; in these plants the numerous stamens are massed in male cones often of considerable size, though smaller than the female cones. In other families, such as the grasses, Cyperaceae, Urticaceae, the number of stamens in each flower is small but the anthers are large. Again, in these flowers the pollen is dry and powdery and does not stick together in small masses as in entomophilous flowers; this enables the pollen to blow about easily. The pollen in this type of flower must be easily removed by the wind; the absence of floral envelopes facilitates this and so do the pendulous catkins (hazel, plane, etc.) which can sway in the wind. In addition the filament of the stamen is usually long so that the anthers hang out of the



flower, and are also versatile (see FLOWER) so that the pollen is easily shaken from them.

Another common characteristic of the flowers in question is that the stigma is much larger and rougher than that of entomophilous flowers and it is freely exposed to the air so as to increase the chance of reception of the pollen; in maize, for example, the stigma is of very great length. In many catkin-bearing plants the flowering stage occurs before the leaves appear, so that accidental interception of pollen by the leaves is avoided. As already stated dichogamy is quite common in anemophilous flowers but protogyny is much more common than protandry.

## INSECT POLLINATION (ENTOMOPHILY)

The special characteristics of entomophilous flowers are the attractive colour of the floral envelope, the presence of scent and of nectar, and of pollen which is not powdery but sticky and is present in comparatively small quantities. The entomophilous is the most common type of pollination in flowering plants and special floral conformations and irregularities adapted to insect visitors are characteristic of the higher families of flowering plants, as will be seen below. The evolution of flowers and of insects must have gone hand in hand; such groups as *Lepidoptera* (butterflies and moths) and *Hymenoptera* (bees, wasps, etc.) could not have existed without the more elaborate and honey-bearing flowers and *vice versa*. Hermann Müller (see *Bibliography*) has divided flowers into various classes according to their degree of specialisation for different insects, so that a brief survey of the types of insects concerned must be given.

**Types of Insects.**—There are five important classes of insects which visit flowers. The *Hemiptera* (bugs, etc.) have a few flower-visiting species but they show no special adaptation to flowers; the *Coleoptera* (beetles) have many species which visit flowers but they have only short tongues (only a few species with a length of 3 to 6 mm.) and so are able to reach only honey which is fully exposed. The *Diptera* (flies) include many species which visit flowers. The *short-tongued* ones (with tongues under 4 mm.) show no special adaptation to a diet of floral origin and are not usually clever enough to find any nectar which is not fully exposed in the flower; many of these flies have also other sources of feeding. The long-tongued flies (such as hover flies or drone flies) have tongues from 4–12 mm. and confine themselves to a diet of nectar, and are clever in discovering it when concealed. The *Hymenoptera* (bees, wasps, sawflies, ants, etc.) include a very large number of flower-visiting forms. Bees are the only long-tongued members of the group, and it is bees which have played the most important part in the evolution of the more complex flowers. The hive bee (*Apis*) and the humble-bee (*Bombus*) have long tongues (over 6 mm.) while most of the other bees have shorter tongues, *i.e.*, less than 6 mm. The “cleverness” of bees, combined with the length of their proboscis, enables them to find and reach nectar which is deeply concealed in the flower. Bees do not confine themselves to sucking nectar from the flower; they also collect pollen (some flowers provide only pollen and no nectar), which is carried in small masses attached to the hairs of the hind legs. The *Lepidoptera* (butterflies and moths) are insects with tongues usually about as long as those of bees, but the hawk moths may have tongues, when unrolled, of enormous length. The British hawk moth, *Sphinx convolvuli*, has a tongue 80 mm. ( $3\frac{1}{5}$  in.) long and some tropical moths a tongue of 300 mm. (12 in.).

**Classes of Flowers.**—The entomophilous flowers have been divided by H. Müller into nine classes based on the structure of the flower and its relation to particular insects.

(i.) Class A. *Flowers with Exposed Nectar*.—In this class come most Umbelliferae, many Saxifragaceae, the bedstraws (*Galium*), ivy (*Hedera*) and such trees as maple, elder and lime. The flowers are wide open and usually small and the visitors are mostly short-tongued; they are rarely visited by bees and butterflies. Such flowers run the risk of the nectar being washed away by rain.

(ii.) Class AB. *Flowers with Partially Concealed Nectar*.—In this class fall the buttercups (*Ranunculus*), the Cruciferae, the strawberry (*Fragaria*) and the willows (*Salix*). The nectar is

protected and concealed by the position of the stamens, by the development of hairs or scales, or by the flower being partially tubular, as in wallflower where the sepals stand erect and give a tubular form to the lower part of the flower.

(iii.) Class B. *Flowers with Fully Concealed Honey*.—In this class are the flowers of many Carophyllaceae (such as *Gypsophila*, *Geranium*), *Polemonium*, blackberry (*Rubus*), eyebright (*Euphrasia*) mint (*Mentha*), heather (*Calluna*). In these the nectar may be concealed by the stamens, by the calyx, by the receptacle becoming hollowed, or by the petals being united to form a sympetalous corolla. The insect visitors are the smaller bees with a few of the longer tongued flies. This type of flower is clearly the most effective of the classes so far mentioned. The bees show a high degree of skill in reaching the concealed honey and mostly confine themselves during a given flight to one or a few species of flower, and thus avoid the great waste of pollen caused by shorter tongued insects, which are liable to carry it indiscriminately from the flower of one species to another.

(iv.) Class B' is an extension of Class B and includes the flowers of the Compositae, most Dipsaceae and some Campanulaceae, in which the flowers have the same length of tube, etc., as Class B, but are aggregated into an inflorescence, which by the uninstructed might be mistaken for a flower, and which acts like a single flower as a unit of attraction.

(v.) Class F. *Lepidoptera Flowers*.—This includes those flowers in which the floral tube has been so deepened that short-tongued insects are excluded altogether and in many cases only *Lepidoptera* can reach the nectar. The alpine moss campion (*Silene acaulis*), for example, is adapted to butterflies, while the bladder campion (*S. inflata*) is adapted to moths and emits a scent at night. To the latter class belong also the honeysuckle (*Lonicera*), tobacco plant (*Nicotiana*), evening primrose (*Oenothera*), and night-scented stock and many others.

(vi.) Class H. *Bee Flowers*, are those which are visited mostly by long-tongued bees, the depth of the tube being 6 to 15 mm. The flowers are also often markedly zygomorphic (*i.e.*, having a special kind of irregularity; see FLOWER), providing a landing place for the bee; others are of such a shape that (as in the snapdragon and broom) it requires an insect like the humble-bee which is not only “clever” but of considerable size and weight in order to open the flower.

(vii. and viii.) The D and K classes of flowers include those adapted to small insects; they are pollinated by flies, beetles and small bees.

Lastly, there is (ix.) the Class Po, *Pollen Flowers*. These provide no nectar, but abundant pollen for which the flower is visited, mainly by bees; examples are *Clematis*, meadowsweet (*Spirea*), rock rose (*Helianthemum*) dog rose (*Rosa canina*), poppy. In some flowers, such as *Cassia*, some stamens provide “food-pollen” for insects, other stamens supply the fertile pollen for fertilization.

**Nectar, Colour and Scent.**—Nectar is a watery fluid secreted by certain parts of the flower and sometimes by other parts of the plant, as in the case of the extra-floral nectaries. It contains a sugar (glucose) sometimes to as much as 25%. It is from the nectar that the bee makes honey, which is a manufactured product with nectar as the raw material. As has already been indicated the position of the nectaries (the nectar-secreting glands) is very various; they may be fully exposed or hidden and deeply enclosed. In some cases the nectar is secreted by one organ and collected in another as in *Viola*, where it collects in the spur but is secreted by appendages of the stamens. In other cases there is no free nectar but the insect must pierce with its proboscis the juicy, sapid cells, which in the case of some orchids line the spur.

The importance of colour in attracting the attention of insects is obvious, but it does not follow that the flowers most striking or attractive to our eyes are those most conspicuous or alluring to the insect. The problem of the colour-sense of insects has been investigated by a number of workers and it seems clear that bees at least can distinguish some colours, such as blue and yellow, and do not merely depend on the different brightness between, say, a deep purple flower and a light yellow one. In the different flower classes (A to H) already defined, there is a tendency to a progres-



sion in colour; the simpler flowers in the A and AB classes tend to be white or yellow, while in the B class blues and purples are found. In class H, the bee flowers, blues and purples predominate, while in class F, the butterfly and moth flowers, pale tints of pink and purple are most common. The special colour markings on flowers, such as the yellow eye of forget-me-not (*Myosotis*), the darker lines on the petals of the violet and pansy, appear to assist the insect to find the nectar and are known as honey guides.

Scent is obviously of great importance and the olfactory sense of some insects such as moths is very much greater than ours. J. H. Fabre showed that moths when out of sight of honeysuckle would fly straight to it from a distance of several hundred yards. K. van Frisch has investigated elaborately the olfactory sense of the honey bee. Bees which had been drilled by association of oil of orange with sugar could pick out this scent from 43 other ethereal oils. As stated by M. Skene (*see* p. 172) the general conclusion is "that colour is the guide to the flower, and that scent is useful in enabling the bee, flying among the many flowers of similar colour, to pick out the species it has formed the temporary habit of visiting." In this it is helped by the sense of form.

#### SPECIAL MECHANISMS OF ENTOMOPHILOUS FLOWERS

**Pollination of Sage.**—Such a plant as the sage (*Salvia pratensis*) has a typical humble-bee flower. The bee alights on the platform formed by the lower lip of the sympetalous corolla and pushes its head down the tube to reach the nectar at the bottom. Each of the two stamens is of special shape; the connective is very large and two-armed, and is hinged to the short filament. The longer arm bears a half anther while the short arm is sterile, the whole stamen having a lever mechanism. The bee, in probing for the honey, comes in contact with the short arm of the lever and in pressing this down brings the half anther at the end of the longer arm down upon its back where the pollen becomes deposited. The flower is protandrous and in a later stage the style elongates and is brought into the same position as occupied by the back of the bee when in contact with the anther. Cross pollination is thus brought about when the bee passes from a younger to an older flower.

**Papilionaceous Type.**—The Leguminosae (Pea family) show a very interesting series of pollination mechanisms. In this familiar type of flower to which the pea and gorse belong, the essential parts of the flower are enclosed in the keel. The nectar is secreted by the inner sides of the lower part of the staminal tube; one of the ten stamens is usually free and at its base are two openings leading to the nectar. The nectar is thus not only carefully concealed but is also at a considerable depth. Cleverness and length of proboscis are thus required so that as might be expected these flowers are bee flowers. An insect visiting the flower alights on the wings, thus depresses them and, as they are joined to the keel, this is depressed also. The stigma and stamens are thus forced out, the stigma usually first so that it has the chance of brushing off pollen from the under-side of the bee and thus being cross pollinated.

There are four different types. (1) Flowers in which the stamens and stigma return within the keel so that repeated visits are possible; examples are the clovers, melilot (*Melilotus*) and laburnum. (2) Flowers that are explosive, since the style and stamens are confined under tension in the keel and when it is depressed they are released with suddenness, thus scattering pollen on the undersurface of the bee. Only one insect visit is thus effective. Examples are broom (*Genista*), gorse (*Ulex*), lucerne (*Medicago*). (3) Flowers which display a *piston mechanism*—the pollen is shed early and the heads of the five outer stamens act as a piston so that the weight of the bee on the keel squeezes a narrow ribbon of pollen through the pore at the apex of the keel. A further pressure causes a protrusion of the stigma which is thus brought in contact with the bee. Examples are lupin (*Lupinus*), rest harrow (*Ononis*) and bird's foot trefoil (*Lotus corniculatus*). (4) Flowers which show a *brush mechanism*, for the pollen is again shed early and the style, which is provided with a brush of hairs, sweeps the pollen in small portions out of the tip of the keel. Flowers of this type usually allow of repeated insect visits.

**Pinch Trap Flowers.**—This type of flower is found in the Asclepiadaceae. The pollen is massed together into pollinia and pairs of these are attached to a sort of clip in which the leg of the insect (bees, wasps, etc.) becomes caught. The pollinia are thus carried away to another flower and are likely to come in contact with its stigmatic surface. *Pitfall flowers* are shown by the cuckoo pint (*Arum maculatum*), a common British plant, and by *Aristolochia* and *Asarum*. In *A. maculatum* there is a spathe surrounding a spadix which bears a fringe of stiff downwardly projecting hairs at the top. These hairs allow the entry of insects but not their return; the insects are thus trapped for a time in the spathe and pollinate the pistillate flowers; later the hairs wither and exit becomes possible. Flies are the common visitors.

**Piston Mechanism of Compositae.**—The flowers of this family show a very efficient pollination mechanism which, with the economy of material resulting from the massing of the flowers into heads and the effective method of seed dispersal, probably explains the dominant position of the family.

**Pollination of Fig.**—The fig shows a very remarkable inter-relationship between an animal and plant. The flowers in the fig are unisexual and are borne in numbers together on the inside of the hollow inflorescence, which opens to the outside by a pore. The swollen and fleshy infructescence (as the inflorescence becomes) is the edible fruit; each "seed" being the product of a single flower and in reality a fruit. The female of a small wasp (*Blastophaga*) enters the inflorescence and deposits eggs in special "gall flowers" incapable of setting seed. The larvae are hatched out and undergo metamorphosis. The male wasps fertilise the female and then die without leaving the inflorescence. The female wasps leave the gall flowers and crawling out through the pore become dusted with pollen from the male flowers in the neighbourhood of the pore. They then enter other figs and pollinate the female flowers, which set seed. The fig and wasp are thus mutually dependent. When Smyrna figs were introduced into California it was found necessary to introduce the caprifig (non-edible fig) containing the wasp *Blastophaga*.

**Pollination of Yucca.**—This is another case of the complete interdependence of a flower and a moth. The large white flowers of this plant emit their perfume especially at night and are visited by a moth (*Pronuba yuccasella*). The female moth (*see* YUCCA-MOTH) collects pollen from the anthers of the flower and kneads it into a pellet about three times the size of its head. It flies to another flower and, piercing the ovary wall with its long ovipositor, lays a few eggs between the ovules. After this it climbs down the style of the hanging flower and presses the ball of pollen into the stigma; by this means fertilisation is ensured. Only a certain proportion of the seeds are destroyed by the developing insects, which, when mature, eat through the fruit wall, drop to the ground and remain dormant in a cocoon until the next flowering season, when the moth emerges. This seems to be the only method of pollination, for in the absence of the moth the plant is said to be completely sterile.

**Pollination of Orchids.**—The orchids show many and complicated adaptations to pollination by insects. A great impetus to their study was given by the publication in 1862 of Darwin's monograph on the various pollination mechanisms exhibited by this group. As is well known, in this flower there is generally only one stamen, which is two-lobed, and the pollen is in the form of two stalked masses, the pollinia which the insect carries away stuck to its head. As the insect flies away, the pollinia, if not already properly oriented, execute such a movement as brings them into position to touch the stick stigma of the next flower that is visited. There are, however, a great many variations in the details of this process. Nectar is not usually secreted by the orchid flower, but to obtain a sweet juice the insect has to pierce a special tissue, usually that of the labellum (the posterior petal), which is often spur-like.

**Heterostylism.**—In some cases the plant bears more than one type of flower. The primrose (*Primula vulgaris*) and the cowslip (*P. veris*) are dimorphic, *i.e.*, some plants have flowers with a long style bearing a knob-like stigma at the mouth of the corolla tube and the five stamens stand half-way down the tube: in others



the flower has a short style with a stigma half-way down the tube while the stamens stand at the top. These two types of flower are known as "pin-eyed" or long-styled and "thrum-eyed" or short styled, respectively. From their correspondence in position, the insect tends to transfer pollen from the thrum-eyed to the stigma of the pin-eyed and *vice versa*. These two types of pollination are spoken of as "legitimate," and Darwin showed that this type produces more seed and more vigorous progeny than "illegitimate" pollination of thrum-eyed stigma by thrum-eyed pollen or pin-eyed stigma by pin-eyed pollen. In trimorphic plants such as the loose-strife (*Lythrum Salicaria*), there are three types of flower, short-styled, long-styled and those with styles of intermediate length. In each type the stamens are in two groups of different lengths; in the first type the stamens are long and intermediate, in the second type they are short and intermediate, and in the third they are short and long. Eighteen possible methods of pollination are possible, six being "legitimate" and 12 "illegitimate." Legitimate unions are found to yield a larger amount of seed than illegitimate.

#### POLLINATION BY AGENCIES OTHER THAN WIND AND INSECTS

In some water plants the pollen is brought to the stigma by the agency of water. In *Najas* the pollen grains sink in the water and are caught by the stigma. In the eel-grass (*Zostera*), the American water-weed (*Elodea canadensis*), and others, the pollen floats on the surface and so reaches the female flowers. In *Vallisneria*, the male and female flowers are on separate plants and the male becoming detached and floating free on the surface of the water, may reach and become entangled with the fixed larger female flowers, with the result that the anthers come in contact with the projecting stigmas.

In some cases animals other than insects are responsible for pollination. In some countries pollination by birds (humming birds, honey suckers and sun birds) plays a considerable part. These *ornithophilous* flowers, as they are called, are not very different from insect flowers, many bird flowers being also visited by insects. A landing place is, however, not necessary, as the birds sip the nectar while hovering. The flowers are scentless, and the styles, stigma and filament often rigid. The colour red seems to be predominant in flowers of this type. Examples of ornithophilous flowers are *Strelitzia regina* in South Africa, species of *Salvia* and *Erythrina* in South America. In Java, species of *Freycinetia* and in Trinidad *Bauhinia megalandra*, are said to be pollinated by bats.

#### SELF POLLINATION (AUTOGAMY)

Self pollination is effected in various ways. In the simplest case the anthers are close to the stigmas, covering these with pollen when they open; this occurs in a number of small annual plants, also in *Narcissus*, *Crocus*, etc. In snowdrop and other pendulous flowers the anthers form a cone around the style and the pollen falls on to the underlying stigmas, or in erect flowers the pollen may fall on to the stigmas which lie directly beneath the opening anthers (e.g., *Narthecium*). In very many cases the pollen is carried to the stigma by elongation, curvature or some other movement of the filament, the style or stigma, or some other part of the flower, or by correlated movements of two or more parts. For instance, in many flowers the filaments are first directed outwards so that self pollination is not possible, but later incline towards the stigmas and pollinate them (e.g., numerous Saxifragaceae, Cruciferae and others); or the style which first projects beyond the anthers, shortens later on, so that the anthers come into contact with the stigmas (e.g., species of Cactaceae); or the style bends so that the stigma is brought within the range of the pollen (e.g., species of *Oenothera*, *Epilobium*, most Malvaceae, etc.). In *Mirabilis Jalapa* and others the filaments and styles finally become intertwined, so that pollen is brought in contact with the stigma. Self-pollination frequently becomes possible towards the end of the life of a flower which during its earlier stages has been capable only of cross-pollination. This is well seen in the case of the flowers of the Compositae, where the stigma lobes later bend round and come in contact with the pollen held by the brush of the style below.

**Cleistogamy.**—The extreme case of autogamy is that of cleistogamous flowers which must necessarily be self-pollinated. The sweet violet (*Viola odorata*), the wood sorrel (*Oxalis acetosella*), *Lamium amplexicauli* and other British plants bear, in addition to the ordinary flowers, small bud-like flowers (cleistogamous flowers) which never open. The pollen germinates in the anthers and the pollen tubes pierce the walls and so reach the stigmas and the ovules are fertilised. Some plants such as *Salvia cleistogama* produce only cleistogamous flowers.

**BIBLIOGRAPHY.**—The classical compendium on flower pollination in English is P. Knuth, *Handbook of Floral Pollination* (Oxford, 1906, original German edition, 1898–1905), where a great mass of data is brought together. Good brief reviews of the subject are given in M. Skene, *The Biology of Flowering Plants* (1924); Kerner and Oliver, *The Natural History of Plants* (1895); the earlier editions (e.g., the 2nd of 1904) of J. C. Willis, *A Dictionary of Flowering Plants*. Most text books of botany give some review of the subject. The earliest work on the subject was C. K. Sprengel's book entitled *Das entdeckte Geheimnis der Natur in Bau und in der Befruchtung der Blumen* (Berlin, 1793); Sprengel's first observation in this field was that of the presence of hairs in the throat of the corolla of a species of *Geranium*, which, he concluded, were for the purpose of preventing the nectar being washed out by rain; from this he was led on to consider the function of corolla markings such as the yellow centre of forget-me-not which he interpreted as honey guides to the insects. For the distinction of flower classes see H. Müller, *The Fertilisation of Flowers* (London, 1883). For the colour sense and olfactory sense of bees see K. von Frisch, *Der Farbensinn und Formensinn der Biene* (Jena, 1914) and *Über den Geruchssinn der Biene* (Jena, 1919). For a review of ornithophilous flowers see F. Werth, "Kürzer Überblick über die Gesamtfrage der Ornithophilie," *Bot. Jahrb.* (1915).

(V. H. B.)

**GLAUCOUS**, a word meaning of a sea-green colour, in botany covered with bloom, like a plum or a cabbage-leaf.

**BOTANIC GARDEN.** The original conception of a botanic garden was that literally implied by the name, that is, a garden, with the plants arranged according to some system of botanical classification. A botanic garden thus differed from a park, where the plants are usually arranged solely with reference to securing a beautiful landscape effect. The primary purpose of a park, moreover, is recreation, while that of a botanic garden has always been science and education. In time, however, these institutions developed along broader and more inclusive lines, and a botanic garden is properly defined as a scientific and educational institution whose purpose is the advancement and diffusion of a knowledge and love of plants.

A collection of living plants, out of doors or under glass, must always remain a major feature of botanic gardens, but the modern institutions possess, in addition, a herbarium, a library, experimental grounds for plant breeding and other investigations, laboratories, classrooms, lecture halls and, in some cases, botanical museums, together with scientific, educational and administrative staffs. Different institutions place the emphasis on different aspects of the work, and this may be determined by climate, area, tradition, resources or ideals.

Botanic gardens have gradually developed by a process of evolution from such gardens as the early olive orchards and the temple gardens, like that, for example, at Karnak, Egypt—one of the earliest of which there is authentic record, dating from the reign of Thotmes III., about 1500 B.C. It seems probable that the very earliest gardens were utilitarian in purpose—for the growing of food and fibre plants and fruit trees. Temple grounds, however, were early planted, and to this practice we are probably indebted for the preservation, until now, of the "maidenhair tree," *Ginkgo biloba*. (See GINKGO.) One of the first gardens, developed for the express purpose of facilitating the study of plants was that of Aristotle, an ardent student of plants, who wrote books on botany, now lost. This garden was in charge of his pupil, Theophrastus, who fell heir to it on the death of the master. It would thus appear that, in modern terminology, the first patron of botany of whom we have record was Aristotle (c. 350 B.C.), and the first "director" of a botanic garden, Theophrastus, who also wrote books on botany.

The history of botanic gardens during the period between those of antiquity and the 15th or 16th century appears never to have been traced in detail. During the 16th and 17th centuries the



herbalists (predecessors of the modern botanists) began to cultivate private gardens for the purpose of botanical study. Perhaps the best known of these is the garden of John Gerard, in Holland. (These private gardens were the forerunners of the modern botanic gardens.) The botanic garden idea spread rapidly in countries of older civilization during the 18th and 19th centuries. There were also vigorous attempts to establish botanic gardens in the United States, as Bartram's garden near Philadelphia, Penn. (1728), Evan's garden, also near Philadelphia (1828, an offshoot from Bartram's garden) and the Elgin Botanic garden, New York city (1801). Notwithstanding the phenomenal growth of the United States, the botanic garden idea was slow to take root, and it was nearly 60 years from the Elgin garden to the establishment of Shaw's garden (now the Missouri botanical garden), at St. Louis, Mo., in 1859. This garden appears to be the oldest existing botanic garden in America organized as an independent institution.

Modern botanic gardens in all countries are organized along closely similar lines. There is a director with a scientific (and sometimes an educational) staff, a head gardener, a number of gardeners and a force of labourers for the maintenance of walks, driveways and lawns. In the case of governmental gardens (e.g., Kew in London, Edinburgh in Scotland, Glasnevin at Dublin, Ireland, Berlin in Germany, Buitenzorg in Java, Singapore, Port-of-Spain in Trinidad, Hope and Castleton gardens in Jamaica, and others) the director reports to a governmental minister or bureau, and the financial support comes wholly or chiefly from governmental appropriations. In the case of independent institutions (e.g., Missouri botanical garden at St. Louis, the new California botanic garden at Los Angeles, the Boyce Thompson southwestern arboretum at Superior, Ariz. and others) there is a board of trustees who administer the permanent funds and other income. Gardens that form integral parts of universities or other institutions (e.g., Cambridge in England, Harvard at Cambridge, Mass., the Hortus Botanicus at Amsterdam, and Brooklyn at Brooklyn, N.Y.) are administered by the trustees of the given institution. A fourth group comprises those gardens which are supported in part by municipal or other governmental appropriations and in part by private funds administered by a board of trustees, as is the case, for example, with the New York botanical garden and the Brooklyn botanic garden. Various botanic gardens in Europe derive their support wholly or chiefly from the city in which they are located, as, for example, Bath (England), Bern (Switzerland), Marseilles (France) and Valencia (Spain).

Among botanic gardens that form an integral part of the botanical departments of colleges and other schools or are closely affiliated with them may be mentioned the following: Aberdeen, Dundee and St. Andrews universities in Scotland, Birmingham, Cambridge and Oxford universities, and the Royal Agricultural college at Cirencester (Gloucester) in England; Trinity college, Dublin, in Ireland; those at the universities of Budapest (Hungary), Czernowitz and Cluj (Rumania), Krakow and Lwow (Poland), Praha (Czechoslovakia), Vienna (Austria); at Ghent and Liège in Belgium; at Copenhagen in Denmark; at the Catholic university in Lille, France; at the medical college and the veterinary college in Lyons, France; at Strasbourg (France); at Madrid (Spain); at the universities of Bonn, Breslau, Göttingen, Halle, Munich and Würzburg in Germany; at Athens (Greece), Groningen, Leiden and Utrecht (Holland); Genoa and Modena (Italy); Kiev, Odessa and Leningrad (Russia); Basel and the Jardins Alpains de l'Université de Grenoble (Switzerland); Nikko and Tokyo (Japan); the Botaniska Trädgård of the University of Helsingfors (Finland); and, in the United States, those of the universities of California (Berkeley), Harvard (Cambridge, Mass.), Smith college (Northampton, Mass.) Mt. Holyoke college (South Hadley, Mass.), Michigan Agricultural college (East Lansing), the University of Michigan (Ann Arbor), the University of Minnesota (Minneapolis), the University of Pennsylvania (Philadelphia) and the Johns Hopkins university (Baltimore). Also, the University of British Columbia (Vancouver). Harvard university maintains a botanical garden in Cuba as well as in Cambridge, Mass.

There are approximately 325 botanic gardens outside of the United States. Among the more notable of these are the following, which are mentioned in the order of age, the year given being the date of their foundation.

**Old World Gardens.**—1. Pisa, Italy (1543), founded by order of the Grand Duke Cosimo de' Medici I. This is one of the earliest gardens devoted to the public study of botany, and became famous under its second director, Andrea Caesalpini. His work, *De plantis libris XVI.* (1583) marks the beginning of modern systematic botany, and influenced botanical science for more than a hundred years.

2. *Musée d'Histoire Naturelle*, Paris (1635), founded by Guy de la Brosse, physician to the French king. Its first name was *Jardin Royal des Plantes Medicinales*, but was changed to the present form in 1790. The garden proper, still generally known as the *Jardin Botanique*, occupies an area of 14 hectares.

3. *Chelsea Physic Garden*, London (1673), was established on the bank of the Thames by the Society of Apothecaries, for the express purpose of advancing the teaching of botany, and of providing study material for research and teaching. In the earlier years the garden grew medicinal plants in sufficient amount to supply the members of the society with crude drugs in commercial quantities. The original plot of 4 ac. was enlarged in 1722 by additional ground deeded as a gift by Sir Hans Sloane with the provision that the growth of drug plants for commerce should cease, and the garden thenceforth be devoted exclusively to scientific and educational work. Its influence along these lines can scarcely be overestimated. Among its famous directors were Philip Miller, author of the classic *Dictionary of Gardening*, and John Lindley (appointed in 1835), author of *Flora Medica* and other important botanical works. Many important publications grew out of the work of the garden, including Curtis's *Botanical Magazine* and *Flora Londonensis*, Lindley and Moore's *Treasury of Botany*, and others. The private library of Charles Darwin is housed in the laboratory building.

4. *Der Staatliche Botanische Garten und Museum*, Berlin-Dahlem, Germany (1679), was established in Schöneberg, near Berlin, as an exhibition or model garden (*Mustergarten*). Here it remained for over 200 years. A new site was chosen at Dahlem where in 1897-1907 the present garden was laid out under the direction of Dr. A. Engler, who was director from 1889 to 1921. The area is approximately 100 acres. It is primarily a research institute for botanical science and instruction of Berlin university. The plantations comprise five main sections: (1) Plant Geography; (2) Morphology—Oecology; (3) The Arboretum; (4) Systematic Botany; (5) Economic Plants. The Conservatories contain a remarkable collection of tender and tropical plants. The Botanical Museum comprises the Herbarium and the public exhibits.

5. *Royal Botanic Gardens, Kew*, near London (1759). The nucleus of the collections at Kew was the plants grown by Lord Capel, who came into possession of Kew house by marriage in 1696. Frederick, prince of Wales, leased the property about 1730, and after his death his widow, Princess Augusta of Saxe Gotha, engaged a former pupil of the Chelsea Garden, William Aiton (q.v.), to develop a physic garden in 1757. From this year Kew ranks as a true botanic garden. The total area is 288 acres. It was Aiton, who inaugurated the plan of sending botanical exploring expeditions to foreign countries. The material collected on these expeditions has greatly enriched the scientific collections at Kew, and also our knowledge of the vegetation of the world from the standpoint, not only of pure science, but of economic botany as well. The gardens (as stated in a Kew guide book) stand in relation to botanical science much as Greenwich does in astronomy. The botanical survey of the empire has resulted in the publication of floras of all the overseas dominions. Among commercial plants distributed by Kew to new centres are bread-fruit, pineapple, banana, tea, coffee, cocoa, rubber, various fibres, timbers and dyes, and quinine and other drugs. The quinine plant (*Cinchona*) was introduced by Kew from South America to India in 1860. Most of the crude rubber used so extensively throughout the world is derived from trees of the Para rubber plant (*Hevea*



*brasiliensis*) raised from seeds collected by Sir Henry Wickham under the auspices of Kew in Brazil in 1875. Kew acts as botanical adviser to all Government Departments. The gardens maintain a school of horticulture for the training of gardeners, and are visited by more than a million people annually. Aiton resigned in 1841 and was succeeded by Sir William Hooker (1841-65), Sir Joseph Hooker, his son (1865-85), Sir W. T. Thistleton-Dyer (1885-1905), Sir D. Prain (1905-22) and Dr. A. W. Hill (1922- ). One of the most important publications is the *Index Kewensis*,—an alphabetical list of every plant name published (numbering hundreds of thousands), with references to the place of publication. This project was originally conceived and financed by Charles Darwin.

Among other important European botanic gardens may be mentioned those at Amsterdam where deVries (*q.v.*), carried on his investigations leading to the formulation of the epoch-making mutation theory, Budapest (1771), Cambridge (1762), Christiania (1815), Coimbra (Portugal, 1773), Copenhagen (1600), Genoa, Hanbury (La Mortola, Ventimiglia, Italy, 1867), Helsingfors (1828), Leiden (1587) Leningrad (1843), Madrid (1755), Rome (1884), Upsala (1787), Ventimiglia (Italy, 1867).

In Asia and the Pacific islands: Tokyo (1638); Calcutta Sibour, (1787); Buitenzorg, Java (1817); Hongkong, Paradeniya, Ceylon (1822); Melbourne, Australia (1842) and Hobart, Tasmania (1844). In Africa: Durban (1849) and Kirstenbosch, Cape Town (1913). In South America: Rio de Janeiro (1808) and Buenos Aires (1892).

**American Gardens.**—*Missouri Botanical Garden* (St. Louis, 1859). This is known locally as "Shaw's Gardens," from the name of the founder, Henry Shaw, who first opened the garden (as a private garden) to the public in 1859. The area is about 75 acres.

The garden co-operates closely with the Henry Shaw School of Botany, at Washington university, St. Louis, and the director of the garden is professor in this school. The founder's will provides that there must be preached annually a sermon on the power, wisdom and goodness of God as shown in plant life. During the administration (1889-1912) of the first director, Dr. William Trelease (*q.v.*), the *Annual Reports*, enriched with scientific contributions, became known throughout the scientific world. Under his successor Dr. George T. Moore (1912- ), the *Annals* were initiated, the scientific and educational work expanded, and a new tract of land (the Gray summit extension, of over 1,500 ac.) outside the smoke zone of the city was secured and developed for the growing of conifers and other plants. In 1926 a tropical station was established in the Panama Canal Zone where orchids and other tropical plants will be grown.

*Arnold arboretum* (Forest Hill, Boston, Mass.; 1872), the living tree museum of Harvard university. The principal collection of trees and shrubs was planted in 1886. The area of approximately 250 ac. includes meadow, hill and valley, and the permanent (endowment) funds are about \$2,000,000. There is a library of about 40,000 vol. and 10,000 pamphlets, and a herbarium of the woody plants of the world of about 300,000 sheets. No undergraduate instruction is given, but special research students are received. Publications: *Journal of the Arnold Arboretum*, *Plantae Wilsonianae*, *Bulletin of Popular Information*, *The Bradley Bibliography* (a 5 vol. guide to the literature of the woody plants of the world before the beginning of the 20th century), and other works. Soon after the death of the first director, Prof. Charles Sprague Sargent (*q.v.*), who served from 1872 to 1927, the office of director was abolished and Prof. Oakes Ames was made supervisor, and Mr. E. H. Wilson, keeper.

*New York Botanical Garden* (Bronx Park, New York city; 1894). This comprises an area of approximately 400 ac.; its permanent funds exceed \$2,400,000. There are two large ranges of conservatories, in one of which is a lecture hall. The museum building houses the public museum exhibits, the herbarium of some 2,000,000 specimens, the library of over 37,000 volumes, together with research laboratories and offices of administration. Courses of free public lectures are given throughout the year, and classes from the public schools visit the garden at frequent intervals for special instruction. The Garden has, from the beginning,

carried on systematic exploration of the West Indies, as well as of continental North America. Its publications include the *Journal* (monthly), *Mycologia* (bi-monthly), *Bulletin* (irregular, and containing the annual reports), *North American Flora* (being published in fascicles), *Memoirs* (irregular), and *Contributions*. The Garden is supported by both municipal and private funds, and has, from the beginning until now (1928) been developed under the directorship of Dr. N. L. Britton (*q.v.*). There is a close affiliation with Columbia University.

*Brooklyn Botanic Garden* (Brooklyn, N. Y., 1910). This includes an area about 50 acres; its work includes anything scientific or educational based upon plant life. Many popular courses are given for the general public both children and adults. Its educational program is probably more extensive than that of any other botanic garden. There is a children's garden and children's green-house and building. Boys and girls frequently take consecutive voluntary instruction for periods of five to ten years, finally entering upon a life work of botany, horticulture, or some other aspect of plant science or industry. The research work is mainly with the experimental aspects of botany (pathology, genetics, ecology, physiology), though including some systematic work. Graduate work done at the Garden is credited toward advanced degrees by New York university. The Garden co-operates extensively with public and private schools. The Library, containing over 12,000 volumes and over 10,000 pamphlets, is open free daily to the public. The herbarium contains: flowering plants, 84,000 specimens; Fungi, 72,000; Bryophytes, 11,000; Algae, 3,000. The conservatories contain tender and tropical economic and other plants. The Garden is supported in part by annual appropriations by the city of New York and in greater part by private funds. It was developed under the supervision of the first director, Dr. C. Stuart Gager (*q.v.*). Its publications include *American Journal of Botany* (monthly), *Ecology* (quarterly), *Genetics* (bi-monthly), *Memoirs*, *Contributions*, *Leaflets*, and *Record* (one number of which comprises the *Annual Report*).

*United States Botanical Garden* (Washington, D.C., 1850). This originally occupied about 13 acres near the Capitol grounds. The National Congress, in 1927, authorized the Secretary of Agriculture to establish a National Arboretum on a tract of about 400 acres lying upon the Anacostia river about four miles north-east of the centre of Washington. The Act provides that, "The arboretum shall be administered by the Secretary of Agriculture, separately from the agricultural, horticultural and forestry stations of the Department of Agriculture, but it shall be so correlated with them as to bring about the most effective utilization of its facilities and discoveries." The plans include a relocation of the old botanic garden.

*Boyce-Thompson Institute for Plant Research, Inc.* (Yonkers N.Y., 1921). This was established by a gift of William Boyce Thompson of approximately \$6,000,000, the larger part of which has been set aside as a permanent endowment fund. The institute was incorporated and the laboratories were opened in 1924. The stated purpose is the carrying out of every phase of research on plant life and the dissemination of information relative thereto. In 1928 a tract of about 325 acres on the eastern edge of Yonkers, was secured for the development of an arboretum, where it is planned to grow every hardy species of woody plant. This collection is primarily to serve as a basis for the study of methods of propagation, pathology, and disease control. Planting was begun in the spring of 1929.

Among other American botanic gardens there is space only to mention The Letchworth Park Arboretum (extending for some distance northward of Portage, N.Y., along both banks of the Genesee river); the Morton Arboretum (Lisle, Ill.), and the botanic gardens at various colleges and universities, among which may be mentioned: Harvard (Cambridge), Marsh (at Yale University, New Haven, Conn.), University of Pennsylvania, Smith (at Northampton, Mass.); Mt. Holyoke (at South Hadley, Mass.); Michigan (at Ann Arbor, Mich.); North Carolina (at Chapel Hill), Havana (Cuba), and Bermuda (Hamilton, Bermuda). (See ARBORETUM.)

(C. S. G.)



**LICHENS** are, with few exceptions, land plants of simple structure. They grow almost everywhere, spreading over soil, rocks, the trunks, branches and leaves of trees, etc., as flat crusts, leafy expansions, shrub-like tufts or pendulous filaments in various colour shades of white, grey, yellow, brown or almost black. The term lichen, a word of Greek origin, was first definitely given to lichens as we know them by Tournefort (1700).

Lichens are of unusual interest in that the vegetative body or thallus is a composite plant formed by the interdependent growth of unicellular or filamentous green or blue-green algae Myxophyceae or Chlorophyceae (fig. 1), with the filaments (hyphae) of one of the higher fungi—Ascomycetes or, in one or two genera only, Basidiomycetes. On this basis of combination or symbiosis there has been evolved a great series of distinctive plants, capable of vigorous life and of reproduction from generation to generation. Phycolichens signify those that contain blue-green, Archilichens those with bright-green algae, designated as lichen gonidia. The fungus is the dominant partner as it provides the fruiting bodies.



FIG. 1.—LICHEN HYPHAE AND GONIDIA. ASSOCIATION OF LICHEN HYPHAE AND GONIDIA X 250. (AFTER BONNIER)

**Lichen Gonidia.**—For long it was accepted that the green bodies in the lichen plant were cells budded off from the colourless hyphae that gradually acquired a green colour. It was known that minute portions of a lichen plant—the soredia—each composed of a few green cells with entangled colourless filaments were agents of propagation. Wallroth (1835), for that reason, coined for the green cells the term *gonidia* to signify their reproductive function (fig. 2). In most lichens there is a gonidial zone near the surface and to that he gave the name *stratum gonimon*. In a lesser number the gonidia are distributed through the thallus (fig. 3). These two types he distinguished as *heteromerous* with distinctive layers, and *homoimerous* where there is no such diversity.

The belief in the genetic origin of the green cells within the thallus held sway for many years, though observations of a disturbing character were not lacking. Agardh (1821) had suggested that they were transformed algae as he had followed the development of the blue-green alga, *Nostoc*, to the complete thallus of the lichen, *Collema*. The view gradually gained ground that the bright-green gonidia of many lichens were comparable to the alga *Protococcus*. The explanation given was that these free grow-



FIG. 2.—THALLUS WITH GONIDIAL ZONE. SECTION OF HETEROMEROUS THALLUS X 500. (AFTER SCHWENDENER)

ing algae were lichen gonidia escaped from the thallus that had continued independent growth. Wallroth spoke of them as "unfortunate brood cells" that could not again form a lichen plant. Finally in 1867 Schwendener published his bold theory that lichen gonidia were true algae imprisoned and parasitized by fungal hyphae. The statement was welcomed by many as enlightening and convincing. Others, among

whom were the renowned Finnish lichenologist, W. Nylander and the British J. M. Crombie, scornfully rejected the new view. The theory was, however, successfully tested by cultures of lichen spores with free-growing algae—first by Rees (1871), then by Bornet (1872) and others who followed the development from spore to fruiting stage, a slow growth of several years' duration.

**Symbiosis.**—The relation between the two organisms was regarded at first as a parasitism of the fungus on the alga, or as *helotism*. Reinke (1873) pointed out the insufficiency of a condition of parasitism to explain the healthy lichen, and he therefore proposed the term *consortium* as a truer conception. A few years later de Bary (1873) suggested *symbiosis* as an adequate

term and it is now generally accepted as a *mutual symbiosis*. This view has been confirmed by culture experiments. In general the alga supplies carbohydrates by photosynthesis, the fungus provides salts and water storage. Symbiosis in lichens is a fairly stable life-balance which may tip, however, to the detriment of one or other of the organisms: there are instances, perhaps more frequent than we have supposed, of gonidia perishing in the grip of the fungi, but there are also cases where owing to some unfavourable condition, the fungus has succumbed while the algae increased enormously. There is no doubt as to the normal healthy condition of the thallus and of both symbionts. The interest in lichen gonidia has of late centred in the globose bright-green alga for many years considered to be a species of *Protococcus*, but that alga multiplies by cell division and is now recognized as the gonidium of only a few lichens. The ordinary lichen gonidium was found by Paulson and Somerville Hastings (1920) to have a massive parietal chromatophore, and to multiply freely and abundantly in the thallus by the free cell formation of aplanospores. The season of greatest increase was from February to April, or after heavy rain following a season of drought; zoospores were not seen in the gonidial state. The sporulating gonidia were most abundant in the actively growing regions. More recently Puymaly (1924) has proposed a new genus, *Trebouxia*, for the alga without and within the lichen thallus. He describes it, however, as possessing a massive stellate chromatophore. In view of Paulson's observations, again renewed, it is impossible to regard the gonidium chromatophore as of stellate form.

**Lichen Algae.**—The algal constituents of the thallus belong to two classes. I. Myxophyceae (blue-green algae) and II. Chlorophyceae (bright-green algae). They are, in general, aerial forms and in a free condition inhabit moist shady situations. Though

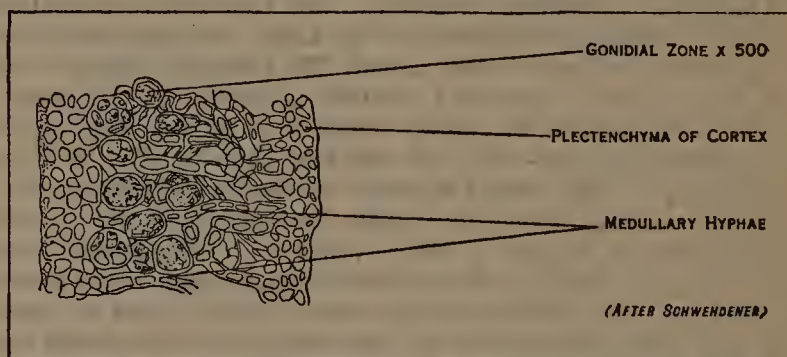


FIG. 3.—THALLUS WITH DISPERSED GONIDIA. SECTION OF HOMOIMEROUS THALLUS X 250. (AFTER B. M. HANDBOOK OF BRITISH LICHENS)

the determination of algal species is somewhat uncertain, the genus can be more easily recognized.

I. Myxophyceae associated with Phycolichens in Collemaceae and other families. The algae of most frequent occurrence are *Gloeocapsa*, *Nostoc*, *Scytonema* and *Stigonema*.

II. Chlorophyceae associated with Archilichens. Those of most importance are the globose algae belonging to the Protococcaceae and *Trentepohlia*, a filamentous alga.

The alga may become modified in the gonidial state: *Gloeocapsa* loses colour, *Nostoc* chains, and *Trentepohlia* filaments may be broken up into cell units.

**Lichen Hyphae.**—These undergo considerable modification as lichen symbionts. The fruiting form indicates their origin as ascomycetous or basidiomycetous, and their affinity can be traced to ancestral groups of fungi. Bonnier (1889) in describing their development from the spores in synthetic cultures noted three distinct types:—(1) clasping filaments with repeated branching which surround and secure the alga; (2) filaments with short swollen cells destined to form several lichen tissues and (3) towards the periphery, searching filaments that form the hypothallus and annex new algae. In five days after germination the clasping hyphae had laid hold of the alga and symbiotic growth had begun. In the growing regions the hyphae remain comparatively thin-walled. In other parts—especially in the cortex, etc.—the walls frequently become thick and gelatinized. In lichens as in fungi there is no true cell structure or parenchyma, but in the cortices of many lichens a pseudo-parenchyma or plectench-



yma arises by the closely packed growth of the septate tips of the hyphae. Plectenchyma also occasionally appears in other parts of the thallus.

Cultures in artificial media apart from gonidia have been made by several workers: by Möller (1887) with *Lecanora subfusca*; by F. Tobler (1909) and by Killian (1925) with *Xanthoria parietina*. Also by Killian and Werner (1924) with the spores of *Cladonia squamosa*. In all cases the results were fairly similar: growth was slow and finally ceased—in *Xanthoria parietina* in eight or ten months. A series of tissues was however observed in the last culture: (1) a dense layer of filaments representing the medulla; above that (2) a looser tissue in the position of the gonidial layer; and (3) a second dense tissue representing the cortex from which arose aerial hyphae. Tobler further records that growth became more lichenoid when the gonidial alga was introduced and the yellow acid parietin appeared in the tissues. Werner (1927) tested hyphal growth on various media and found that galactose was the most advantageous food supply. Organic nitrogen was added as peptone and asparagin, inorganic as nitrate of ammonium. Growth was slow, but the addition of gonidia to the culture retarded it yet more, so that the algae gained in numbers.

### MORPHOLOGY

The main interest in morphology lies in tracing the effect of symbiosis on development. The fungus as the dominant partner provides the structure of the thallus but the variety of forms evolved is due to the necessity of securing light and air to enable the alga to carry on the work of photosynthesis.

**General Structure of Ascolichens.**—In these there are two main types of thallus:—(1) the *stratose* which includes flat spreading plants, crustaceous or foliose, in which the upper surface alone is exposed to light; and (2) the *radiate* which in the lichen competition for sunlight and space has developed upwards from a rooting base to shrub-like branching fronds or pendulous filaments.

(1) The simplest stratose lichens consist of a film of loose hyphae with scattered gonidia. In further advanced species there is a more bulky thallus formed of an upper cortical protecting layer, generally of dense hyphae with more or less swollen walls and with the lumen of the cells almost obliterated (decomposed cortex); beneath the cortex a gonidial zone of massed gonidia and intermingled slender hyphae, the latter passing downwards to form a loose medulla. Projecting hair-like hyphae anchor the plant to the rock, tree or soil. Fig. 4. The upper surface may be smooth or uneven, or seamed and cracked into small compartments called areolae. Not infrequently the crustaceous thallus is wholly embedded in the substratum as in Graphidaceae. Such lichens on trees are termed *hypophloeodal* in contrast to the surface or *epiphloeodal* forms, a stain on the bark usually indicating their presence; the fructifications are formed on the surface. Similarly rock lichens are *epilithic* or *endolithic*. The latter live in limestone, which they penetrate to various depths. Friedrich (1906) noted in an immersed species, *Biatorella simplex*, a slight cortical layer, below that a zone of gonidia 600–700  $\mu$  in thickness, while the medullary hyphae reached a depth of 12mm. An instance has been recorded of a lichen penetrating to 30mm. below the surface. Still higher in development are the squamulose thalli of tiny leaflets and the larger foliose (fig. 5) forms in both of which the thallus is raised from the substratum partly or entirely and in which the free under-surface also acquires a protecting cortex which generally repeats that of the upper-surface—either of decomposed cells, of plectenchyma, or of hyphae parallel with the surface (fibrous cortex). Stratose lichens start from a centre, the growing tissue is situated in the gonidial zone and the greatest increase is at the periphery, the lichen gradually enlarging on all sides, in some to a size of one foot or more in diameter. Growth is continuous, but divisions may arise that are imbricate and leaf-like. In squamulose forms the squamules arise in succession from



AFTER B. M. HANDBOOK OF BRITISH LICHENS  
FIG. 4.—CRUSTACEOUS LICHEN (*LECANORA VARIATA*) X 50

the spreading hypothallus—the travelling ground hyphae. Foliose forms are attached at irregular intervals by rhizinae.

(2) Radiate lichens, upright fruticose forms (fig. 6), start from a rooting base; the fronds are exposed to sun and air on all sides and the structure is alike round the whole surface. The cortex is of several types:—of decomposed cells, of densely packed, fastigiate hyphae or of longitudinal, thick-walled fibres. All these variations give strength and pliancy to the fronds. Other strengthening structures are the “sclerotic” fibres which extend up the frond either just within the gonidial zone as in *Ramalina* or, as in *Usnea*, in one strong chondroid central strand of great toughness and strength. Growth in radiate lichens is apical or intercalary. Fronds of *Rocellae*, *Ramalinae*, etc., reach a height of several inches; pendulous lichens often grow in long streamers: a length of ten metres has been recorded for *Usnea longissima* in the tropics.



AFTER B. M. HANDBOOK OF BRITISH LICHENS  
FIG. 5.—FOLIOSE LICHEN (*PARMELIA CAPERATA*)

In *Cladoniae*, the cup lichens, there is a double thallus: leaflet squamules of stratosse structure, with upright stalks or *podetia*, frequently widening to a cup or *scyphus* at the top (fig. 7). The podetium becomes hollow in time but is firm and strong owing to the sclerotic fibres that line the central tube. Fructifications are borne on the tips of the podetia, or on the edges of the scyphus, which seems to indicate that the podetium originated as a fruit stalk. There is great variety of form, texture and colour in each of these main groups.

**Special Lichen Structures.**—*Cyphellae*. There are no stomata in lichens, but ample provision is made for aeration and for gaseous exchange. Definite aeration structures (fig. 8), cyphellae or pseudo-cyphellae pierce the thick under-cortex of the Stictaceae. They are small and cup-like, in cyphellae with an overarching margin; the base rests on the medulla and the cup is filled with small loose cells. Pseudo-cyphellae lack the cup margin. In other lichens there occur dot-like openings; the lines between the areolae admit air, or the surface is seamed by cracks and delicate reticulations; soredial openings are present in many species, and in *Parmelia exasperata* there are true breathing-pores—minute cone-like outgrowths, open at the summit.

**Cephalodia.** These occur as excrescences on the thallus of Archilichens (with bright green gonidia), and always contain blue-green cells, mostly *Nostoc* or *Scytonema*. They are small bodies of various form and size from the minute pustules on the surface of *Peltigera aphthosa* (fig. 9) to the coral-like masses on *Lobaria laciniata*. Blue-green cells alight by chance on the thallus and the cortical hairs grow out and gradually form a cortex round them. In a few instances there are groups of blue-green cells which are absorbed into the thallus by the under-surface, and a layer of blue-green algae, below the normal bright green zone in *Solorina crocea*, also rank as cephalodia. These alien bodies seem to indicate an ancestral association of the particular lichen with blue-green gonidia, the power to combine having persisted along with the presumably more recent symbiosis with the bright-green alga.

**Soredia.** As already indicated these are minute portions (hyphae and gonidia) that break away from the parent thallus and serve for propagation of species. The simplest types are diffuse soredia that in certain conditions of shade or moisture cover the surface of the plant. More defined forms are termed *soralia* which arise by the upward push of hyphae in the gonidial zone, and emerge as roundish or oblong bodies packed with soredial granules. These multiply and, as they become detached, are easily dispersed. Soralia are more or less specifically constant in form and size and in their position on the surface or margins of the lobes.



AFTER B. M. HANDBOOK OF BRITISH LICHENS  
FIG. 6.—FRUTICOSE LICHEN (*RAMALINA FRAXINEA*), REDUCED 1/2



**Isidia.** Many lichens are rough on the surface owing to small outgrowths called isidia. So noticeable are they that Acharius established the genus *Isidium* to include isidiose lichens. They are cortical structures and begin generally as a small swelling or wart: they are upward extensions of the tissues and the cortex is continuous over their surface; sometimes they are darker in colour than the normal thallus as in *Evernia furfuracea*.

**Structure of Basidiolichens.**—There are three genera recorded in this group of tropical lichens: *Cora*, *Corella* and *Dictyonema*. The gonidia, *Chroococcus* or *Scytonema* are Myxophyceae. *Cora* and *Dictyonema* are of a thin bracket-like form; they grow on the trunks and branches of trees, very rarely on the ground, and are attached by rhizinae. No proper cortex is formed, but in *Cora* the hyphae take an upward direction towards the surface where they become horizontal, so that a compact protective tissue lies over the top; the gonidia (*Chroococcus*) from a zone at the base of the upward hyphae. In *Corella* and *Dictyonema* the *Scytonema* trichomes retain their form and are surrounded by the lichen hyphae.

Basidiolichens are related to the fungal family Thelephoraceae: the fructification is by basidiospores borne on the under-surface of the thallus.

#### REPRODUCTION

Lichens with few exceptions (Basidiolichens and primitive indeterminate forms) are Ascolichens, their method of reproduction corresponding to that of Ascomycetes, i.e., by the production of ascospores in open or closed ascophores—apothecia or perithecia. In the slow-growing symbiotic plants these fruit bodies have been provided with special protective tissues that secure prolonged spore formation, differing in this respect from the fugitive ascophores of fungi.

**Apothecia.**—In lichens these are of several forms to which special names have been given:—ardellae, the irregular spot-like fruit of Arthoniaceae; lirellae, elongate, slit-like, dark-coloured bodies in Graphidaceae; in the larger majority of lichens open discoid apothecia. Those surrounded by a protective thalloid margin are called lecanorine (fig. 10), such as occur in the genus *Lecanora*. Those consisting solely of hyphal tissue surrounded by a hyphal or "proper margin" only as in *Lecidea* are described as lecideine (fig. 11). If that margin is obscure with the disk often brightly coloured they are biatorine, as in the sub-genus, *Biatora*.



AFTER B. M. MONOGRAPH OF BRITISH LICHENS  
FIG. 8.—SECTION OF THALLUS OF STICTA, WITH CYPHELLA ON UNDER-SURFACE MUCH MAGNIFIED

These are true distinctions, and are of value in the determination of genera and species. The difference is due to their origin in the thallus: in the lecanorine series gonidia are carried up with the developing fruit, and algal cells extend along the base and, entering into the "thalline margin," surround the apothecium. The lecideine tissues, solely hyphal, pass up through the gonidial zone, pierce the cortex and expand above it, the outer sterile hyphae forming the protective "proper margin." Minor differences in growth occur, with different types of apothecia—sessile or stalked, etc., and in size from a minute body to one of over three centimetres in width according to the genus or species of lichen. The disk or thecium is composed of a compact series of filamentous upright simple or branched paraphyses and of asci—club-like structures within which eight spores (fewer or more numerous) are produced by free cell formation. These, constituting the hymenium, are subtended by a layer of tissue, the hypothecium; the tips of the paraphyses projecting above the asci form the

epithecium, generally coloured; the surrounding sterile filaments represent the parathecium; the thalline margin when present forms the amphithecium.

**Perithecia.**—These differ from the apothecia in being comparatively small, globose or pear-shaped, closed bodies immersed or semi-immersed in the thallus, and opening above by a pore, the ostiole. When the outer dark wall is continuous it is described

as entire, and when absent at the base as dimidiate. In some genera the paraphyses dissolve as the asci mature.

Apothecia and perithecia are long lived like the thallus and may produce spores continuously or at definite seasons for several years, in *Solorina saccata*, for instance, over a period of two to four years, as observed by Hilzter (1926).

#### Spermogonia or Pycnidia.

—These are small closed bodies outwardly resembling perithecia; the hyphae that line the interior walls bud off minute pycnidiospores. As spermogonia they were considered of great importance as the male organs that produce the spermatia. There is no reliable evidence of their sexual nature and they are now generally classified as pycnidia resembling similar bodies that form a secondary stage in the fruit cycle of the Ascomycetes. It has been proved that the spermatia germinate and produce hyphae, a characteristic of spores.

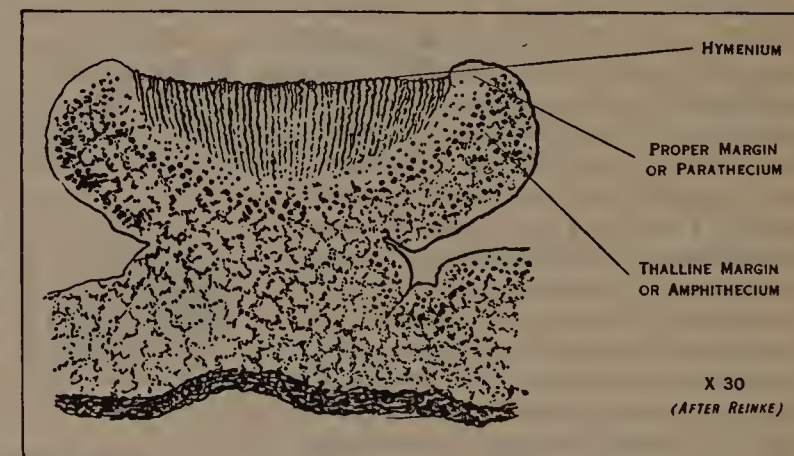
FROM J. BABIKOFF, "DU DÉVELOPPEMENT DES CÉPHALODIES SUR LE THALLUS DU LICHEN PELTIGERA APHTHOSA," NOFFIN BULLETIN (ACADEMY OF SCIENCE, U.S.S.R.)



FIG. 9.—CEPHALODIUM OF PELTIGERA APHTHOSA EARLY STAGE, MUCH MAGNIFIED

**Cytology.**—This aspect of reproduction has excited great interest since Fuisting (1866) observed in a crustaceous *Lecidea* the fruit primordium or ascogonium as a coiled hypha. Stahl (1877) announced the further discovery in a *Collema* of a trichogyne, a filament that travelled upwards from the ascogonium and emerged above the surface. He noted also an empty spermatium (pycnidiospore) adhering to the tip of the trichogyne after presumed fertilization. Other workers made similar observations both in gelatinous and in non-gelatinous lichens, and in open and closed fruits. Copulation with the spermatium has also been demonstrated but the behaviour of the spermatial nucleus has escaped observation. The ascogonium may be a coiled hypha or simply a complex of cells distinguished by their richer

contents, and changes in these cells have been observed that seem to imply spermatial fertilization. It may be that in some lichens fusion takes place between neighbouring cells in the ascogonium: F. Bachmann (1912) found that copulation took place deep down in the thallus of *Collema* sp. between an internal trichogyne and a free spermatial cell. Apogamy, however, undoubtedly prevails in many lichens: either no trichogynes are formed or they fail to reach the surface and fertilization by spermatia is doubtful. Zahlbruckner (1924) has expressed the opinion that reproduction



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FIG. 10.—SECTION OF LECANORINE APOTHECIUM, (*LECANORA SUBFUSCA*)

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by sexual organs—present in the more primitive lichens—tends to die out in more developed forms. The whole subject bristles not only with the difficulties of observation in these slow growing plants, but also with the perplexities of interpretation: the function of the lichen trichogyne, a multispetate hypha of vigorous growth, is not understood; but it may be of some service to the deep seated ascogonium. From the ascogonium arise the hyphae that are destined to form the asci. As in fungi the nuclei of two adjacent cells at the tips of these hyphae fuse and become the definitive nucleus of the ascus. There are normally eight spores, but the number varies in different genera and species from one, as in *Varicellaria*, to the large numbers in *Acarospora*. They are colourless or brown, and simple, variously septate or muriform, and they differ in size from a few microns in *Acarospora*, etc., to the large one-septate spore in *Varicellaria* ( $350 \times 115 \mu$ ). Large simple spores, as in *Pertusaria*, are multinucleate. Spore ejection is brought about by pressure of the paraphyses when moistened.



FROM A. L. SMITH, LICHENS (UNIVERSITY PRESS, CAMBRIDGE)

FIG. 11.—SECTION OF LECIDEINE APOTHECIUM (LECIDEA PARASEMA) (AFTER B. M. HANDBOOK OF BRITISH LICHENS)

### PHYSIOLOGY AND BIONOMICS

**Cells and Cell-contents.**—In the study of lichen physiology attention must be given to the activities of the symbionts as well as to those of the symbiotic plant. Gonidia do not greatly differ from the allied algae growing in the open: they possess chloroplasts, and form starch by photosynthesis. Mameli (1920) and Tobler (1923) demonstrated minute granules of starch on the outside of the gonidia—a ready food for the fungus. The hyphal cells have been more affected by symbiosis, and a much slower growth than in fungi has become a fixed character as proved by artificial cultures. The cell-walls, as in fungal tissues, are formed of hemi-celluloses, chitin being present in nearly all lichens. There is no true cellulose, but a substance, lichenin ( $C_6H_{10}O_5$ ), allied to starch, has been demonstrated as well as a slightly different substance, isolichenin, the latter proved by Ziegenspeck (1924) to be a reserve material. Amyloid hyphae giving a blue reaction with iodine are present in the medulla of several species. Swollen cells filled with oil, probably an excretory substance, occur in many lichens especially in limestone species. Oxalic acid is also frequently found in lichen tissues in the form of crystals, small granules, or in large clear masses as in *Pertusaria communis*.

**Lichen Acids.**—These are the most interesting and characteristic of lichen products. They are deposited on the outside of the hyphal cells as minute coloured specks or as colourless substances, and show a wide range of chemical formulae and a great variety of crystalline form. They are the product of the symbiotic plant as was proved by Tobler (1909) in his cultures of lichen tissues. Many of them are bright yellow, orange or red, and give the clear pure tone of colour to many familiar lichens. They are strongly influenced by light: *Xanthoria parietina*, a brilliant yellow plant in full exposure, becomes grey green in the shade, with a small acid content. Some of these acids are rare, others are widely distributed, e.g.—usnic acid, found in some 70 widely diverse species; atranorin, first discovered in *Lecanora atra*, in about 70 species; salazinnic acid is equally common. They are abundant chiefly on well-aerated portions of the thallus—the soredial hyphae, the outer cortex, the loose medullary tissue, and on the disc of the apothecia.

**Chemical Grouping.** The acids have been arranged by Zopf (1907) in 1, the fat series and 2, the benzole series.

1. The fat series. Zopf includes five groups in this series: three of the series are colourless substances; the coloured include vulpinic acid from the yellow lichen, *Letharia vulpina*, stictaurin deposited in orange-red crystals on the hyphae of *Sticta aurata*, and rhizocarpic acid obtained from the yellow lichen *Rhizocarpon geographicum*.

2. The benzole series, with two subseries—orceine and anthra-

cine derivatives. The colourless orceine contains the colouring principle of commercial orchil. In the anthracine derivatives some of the acids are also coloured, such as parietin from *Xanthoria parietina* and solorinic acid from *Solorina crocea*.

The question has been debated as to the service rendered by the acids: to some extent they protect the plants from wholesale destruction by snails, insects, etc., as they render the thallus more or less unpalatable. Goebel (1927) has demonstrated that they are also a protection against water-logging. He found that out-growths of hyphal hairs, cilia, etc., formed efficient water conductors, but if acids were abundant they remained dry: when the acids were removed by chemical means saturation was easily achieved. As acids are present on all aerated portions, they must be a powerful aid in keeping the air-channels open and thus serve a useful purpose.

**General Nutrition.**—Water is supplied by rain, mist or dew, mist being the most favourable for lichen requirements (Stocker 1927). Dew is important in extremely dry localities such as deserts. Inorganic substances are obtained to some extent from the substratum but mainly from air borne particles. Organic food is provided by the algae or may be procured by the hyphae from humus, etc.

Lichens show marvellous resistance as regards heat or cold. They survive the high temperatures of direct illumination and they endure seasons of extreme cold on mountains or in the polar zone. It is to their power of drying up to a condition of latent vitality that they owe this resistance. Light that can penetrate the thickened cortex and reach the gonidial zone is essential, but the same dense cortex protects the gonidia from too intense sunlight as do the acids and pigments. Light is of first importance in fruit formation, and the fruit bodies are therefore situated on well lighted portions of the thallus.

**Colour of Lichens.**—Soft grey colours predominate, the thick cortex and the underlying gonidia combining to produce this effect; when wetted the cortex becomes transparent and the green colour is more evident. Acids and pigments, the latter usually some shade of brown, give various colours from yellow to brown or almost black. Strong sunlight induces the formation of both acids and pigments, and intensifies colour as seen in exposed situations. Blue, violet or red colours occur more rarely, and generally in connection with the fruiting bodies. Some lichens become rust-coloured by infiltration from an iron soil. It is only when we compare untouched nature with the ugly gash of recent quarrying that we realize the beauty given to the rocks by the variety of lichen colouring.

**Bionomics.**—The response of lichens to their environment is intimately associated with their physiological properties. Their scanty subsistence entails slow development though a few may be ranked as relatively quick growers—mostly soil lichens in touch with moisture. Such are *Peltigera canina* that spreads over damp lawns, etc., and crustaceous forms such as *Baeomyces* spp. *Lecanora tartarea*, and *Lecidea uliginosa*; the latter has been known to spread over an area several feet in diameter in one season, and has been reported as a pioneer plant forming a dark film over sand dunes in Alberta. But in many lichens growth is often almost stationary: the large foliose *Lobaria pulmonaria* and the crustaceous *Rhizocarpon geographicum* have been observed to make practically no advance during a period up to 50 years. Accurate measurements of more active *Parmeliae*, etc., have given a general increase of 1 cm. per annum; their fruiting bodies require in general four to eight years to develop.

Lichens do not grow on friable rocks or on peeling bark. They require, for the first stages at least, a substratum to which they can be firmly attached by filaments or by rhizinae. In fruticose branching and straggling forms compactness is often secured by *haptera*, which form a bridging connection between the fronds of the same lichen or to other vegetation, as for instance, *Cladonia sylvatica*, which becomes detached from the soil and adheres to the growing heather, thus securing not only attachment but light and air. Some few species become loose and continue growth while they drift about as erratic lichens. Several *Parmeliae*, *Alectoriae*, and *Lecanora esculenta*, etc., are erratic forms.



## PHYLOGENY AND CLASSIFICATION

**Phylogeny.**—It would be interesting to know when the symbiotic plant originated and whether the first association of the fungus was with Myxophyceae or Chlorophyceae, but lichens, owing to the gelatinous nature of the thallus, become soft in water and there is little or no evidence in the rocks as to their antiquity: there is only a doubtful record of an *Opegrapha* in Mesozoic chalk. It is concluded from their elaborate morphology and physiology that they are very old plants, but the symbiotic organism—the lichen—is obviously of more recent descent than its component ancestors. Both symbionts are polyphyletic in origin: the algae are blue-green or bright green; the hyphae belong to various phyla of the fungi from which they are late derivatives. Basidiolichens are related to one fungus family, Telephoraceae; Ascolichens to Ascomycetes and to several distinct phyla within that class. There is no haphazard agglomeration of forms in the lichen group, but a closely related and easily recognized series of plant phyla. The ascophore, which marks the phylum, has undergone considerable alteration which is recognized in classification. Phylogenetic development has, however, mainly taken place in the thallus which presumably began as a loose association of straggling hyphae with algal cells. It progressed to the definite crustaceous structure, and finally to the foliose and fruticose lichen. The greatest advance must have occurred when the thalline particle took an upward direction—a small outgrowth that was to develop into numerous forms.

The intimate relation between lichens and fungi is evident in the species that have remained on the border line. Some with scanty thallus appear to lose the algal symbiont as the ascophore matures, and the hyphae apparently revert to saprophytism as exemplified, for instance, in *Calicium*, a lichen genus, with *Myco-calicium*, the fungal counterpart. Others classified now as lichens and now as fungi live on an alien lichen thallus though not always as simple parasites; in a number of cases their hyphae penetrate the thallus and draw sustenance by symbiosis with the algal cells: these have been designated half-parasites. Lichen thalli are, however, a favourite host for many micro-fungi.

The main divisions of Ascolichens are traced to their fungal ancestors by the form of the ascophore:—

Lichen Series	I. Pyrenocarpineae	} to Pyrenomycetes
	II. Coniocarpineae	
	III. Graphidineae	to Hysteriaceae
	IV. Cyclocarpineae	to Discomycetes

Within these series is represented a number of phyla with an orderly progression of thalline structure. Both types of gonidia are sometimes represented in the same phylum and even in the same family e.g., Stictaceae.

The leading phyla of the different series are:—

I. PYRENOCARPINEAE. In this are included phyla of Phycolichens and Archilichens. In the former crustaceous only; in the latter advancing from the crustaceous Verrucariaceae to the squamose or lobed Dermatocarpaceae: a large and varied series.

II. CONIOCARPINEAE. An isolated group characterized by the *mazaedium* type of ascophore—half closed and filled with loose spores at maturity—mostly crustaceous with a few rare squamulose genera, and a world-wide fruticose genus, *Sphaerophorus*.

III. GRAPHIDINEAE. A large series with *Trentepohlia* as gonidium. The progression is from crustaceous forms to the fruticose *Rocellae*.

IV. CYCLOCARPINEAE. With phyla both of Phycolichens and Archilichens. There is a somewhat limited type of thallus in the Phycolichens; the foliose structure is not however uncommon and reaches high development in *Sticta* and in *Peltigera*; fruticose structure is rare.

In the Archilichens there are three great phyla:—

I. LECIDEALES. These are distinguished by the discoid fruit with proper margin only, and include many crustaceous genera, foliose Gyrophoraceae and the almost fruticose Cladoniaceae.

II. LECANORALES. Fruit with a thalline margin: the most numerous and most highly developed phylum, from the lowest to the highest development not only in form and size, but in the

special thalline structure. (See section, "Morphology," p. 30).

III. POLARILOCULARES. A phylum including all types of structure but with a distinctive and characteristic spore—ellipsoid and mostly one-septate, with the median septum becoming so thick that the spore loculi are often relegated to minute spaces at the tips, hence the name *polarilocular*. A delicate canal passes through the thickened septum and forms a connection between the polar cells.

**Classification.**—Basidiolichens are few in number and now present no problems. It is mainly with Ascolichens that workers have been concerned. Before the true nature of lichen plants was understood, many attempts had been made to classify them in relation to each other and to other members of the plant kingdom—to mosses, hepatics or algae. Tournefort (1700) placed them all in one genus *Lichen*, and was followed by Linnaeus (1753). Knowledge of their number and variety increased, and Acharius (1803) gave diagnoses of 23 genera with their included species. Nylander (1854) issued what he considered a final statement on lichen families and genera and of their relationships. His arrangement began with those nearest akin to algae, gelatinous blue-green forms, and wound up with those he considered to be most like fungi—the Pyrenocarpineae. Later students have worked on this basis and now a system of classification has been achieved that largely satisfies modern views. The arrangement of lichens in a natural order has presented great difficulties: it is by following the lines of development as outlined above that a way through the maze of forms—like and unlike—has been reached. The four series of Ascolichens, for instance, are marked by fruiting characters. These are subdivided into families (58 in number) largely on the structure of the thallus. The genera in these families are distinguished by minor differences of thalline though mainly of fruiting characters.

## DISTRIBUTION AND ECOLOGY

**Distribution.**—Lichens are widely distributed: members of nearly all the different families are to be found in every quarter of the globe. Winds or other agencies carry the spores of thalline particles immense distances, and these grow to full stature when they alight on a favourable substratum. It is impossible at the present stage of faulty co-ordination of knowledge to reckon their numbers, but many thousands have been recorded, and new families, genera and species are constantly being discovered. Some lichens flourish best in temperate zones, others in tropical regions, a few are restricted to polar areas, the same species appearing both in the Arctic and Antarctic. They grow best where they can secure light: they are abundant on the tundra or on rocks and walls with a sunny exposure; but a few are shade-plants and grow even in caves. Some can withstand the heat and scanty rainfall of the desert and others advance to the limits of perpetual snow. A fairly large number are cosmopolitan; a lesser number are endemic in larger or smaller areas.

**Ecology.**—Though self-supporting, lichens exhibit a considerable choice of habitat and form more or less constant associations of lichens only or with other plants. They are the pioneers of vegetation and soil-formation. By their delicate filaments they cling to the rock surfaces which they gradually penetrate and disintegrate. By mechanical action due to alternate wetting and drying of the gelatinous hyphae a sucker-like detachment of minute rock particles is constantly taking place (Fry 1924; 1926); by chemical action the acids discharged by the hyphae (carbonic, oxalic or lichen acids) dissolve the hardest rocks and even old window glass. The detached particles and the humus of cast-off portions of the thallus, together with blown dust, form a nidus for other vegetation—mosses and flowering plants—and mixed associations arise. The chief ecological factors are the types of substratum: the associations or communities are therefore naturally divided into:—1, arboreal and lignicolous, 2, terricolous, 3, saxicolous and 4, localised communities such as maritime lichens. Within these great groups there are minor associations influenced by the kind of bark, the nature of the soil (sand, clay or humus) the character of the rock (siliceous or calcareous) and also by conditions of temperature, moisture and exposure. A very dis-



tinct association is that of nitrophilous lichens: it constantly occurs on any kind of habitat in places frequented by birds and small mammals, and near to farm-yards or on road-sides where the dust is mixed with nitrogenous animal matter. As in other plant communities there is a struggle for place and light. Crustaceous species are invaded and ousted by those of thicker or squamulose thallus or by the larger foliose species. Some mischance may in time dispossess them all and colonization begins afresh. Leaf lichens so abundant in the tropics also form distinctive associations. Lichens are rare or absent in the neighbourhood of large towns or industrial areas owing to the impure and smoke-laden atmosphere.

#### ECONOMIC AND TECHNICAL

Lichens occupy a not unimportant place in the economic field. Mites and other small insects, caterpillars and slugs feed on them especially when they are moist and the acids not too pronounced. Petch has stated that they are the staple food of the black termites in Ceylon. Abbé Hue considered that the abundance and perfect development of lichens in the Antarctic was due to the absence of insect life. In northern latitudes several kinds, for example *Cladonia alpestris*, are of great service as provender for domestic animals. *Cladonia rangiferina*, the reindeer moss, is the special food of the reindeer. In times of scarcity it has been found advantageous to grind up lichen thalli after elimination of acids, and to mix the powder with meal for human consumption. *Lecanora esculenta*, a rock lichen and often erratic, is abundant in eastern deserts and has been similarly used: it has been considered that that lichen was the manna of the Israelites. Species of *Umbilicaria* and *Gyrophora* called *tripe de roche* have been used by Arctic explorers to stay the pangs of hunger. *Gyrophora esculenta*, an eastern maritime rock lichen is greatly esteemed as an edible plant both in Japan and in China.

Their value in medicine rested in the past on a somewhat fanciful basis—that of the “doctrine of signatures”: certain characteristics of form by their resemblance to organs of the body, were considered to indicate curative properties. Some very bitter species such as *Pertusaria faginea* served as a substitute for quinine. *Cetraria islandica*, the “Iceland Moss,” owing partly to its gelatinous consistency has been used with good effect in chest troubles, and is now the only lichen recognized in the British Pharmacopeia.

Their use as dye-plants has been known from the earliest times, and before the discovery of aniline dyes the rich and varied colours obtained from lichens were highly valued. The colouring principle of the dyes is contained in the peculiar lichen-acids. Treatment with an alkali is generally necessary to extract the colour; mordants are frequently used. With some lichens, boiling the plants with the material to be dyed is sufficient to secure the desired colour. The dyes can be used only on animal fibres such as wool and silk; they have no effect on linen or cotton. Purple lichen dyes—orchil, litmus or cudbear—are obtained from *Rocella tinctoria*, a maritime lichen, *Lecanora tartarea* and a few others. Other serviceable colours are the varied yellows and browns so much used in home or village industries. But abundant though dye lichens are, they can only furnish a limited quantity.

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(A. L. SM.)

**GRASSES**, a group of plants possessing certain characters in common and constituting a family (Gramineae) of the class Monocotyledons. It is one of the largest and most widespread and, from an economic point of view, the most important family of flowering plants. No plant is correctly termed a grass which is not a member of this family, but the word is in common language also used, generally in combination, for many plants of widely different affinities which possess some resemblance (often slight) in foliage to true grasses; e.g., knot-grass (*Polygonum aviculare*), cotton-grass (*Eriophorum*), rib grass (*Plantago*), scorpion-grass (*Myosotis*), blue-eyed grass (*Sisyrinchium*), sea-grass (*Zostera*). The grass-tree of Australia (*Xanthorrhoea*) is a remarkable plant, allied to the rushes in the form of its flower, but with a tall, unbranched, soft-woody, palm-like trunk, bearing a crown of long, narrow, grass-like leaves and stalked heads of small, densely-crowded flowers. In agriculture the word has an extended signification to include the various fodder-plants, chiefly leguminous, often called “artificial grasses.”

The first attempts at a classification of plants recognized and separated a group of *Gramina*, and this, though bounded by nothing more definite than habit and general appearance, contained the Gramineae of modern botanists. The older group, however, even with such systematists as Ray (1703), Scheuchzer (1719), and Micheli (1729), embraced in addition the Cyperaceae (Sedge family), Juncaceae (Rush family), and some other monocotyledons with inconspicuous flowers. Singularly enough, the sexual system of Linnaeus (1735) served to mark off more distinctly the true grasses from these allies, since very nearly all of the former then known fell under his Triandria Digynia, whilst the latter found themselves under his other classes and orders.

**Structure.**—The general type of true grasses is familiar in the cultivated cereals of temperate climates—wheat, barley, rye, oats, and in the smaller plants which make up pastures and meadows and form a principal factor of the turf of natural downs. Less familiar are the grains of warmer climates—rice, maize, millet and sorgho, or the sugar-cane. Farther removed are the bamboos of the tropics, the columnar stems of which reach to the height of forest trees. All are, however, formed on a common plan.

**Root.**—Most cereals and many other grasses are annual, and possess a tuft of very numerous slender root-fibres, much branched and of great length. The majority of the members of the family are of longer duration, and have the roots also fibrous, but fewer, thicker and less branched. In such cases they are very generally given off from just above each node (often in a circle) of the lower part of the stem or rhizome, perforating the leaf-sheaths. In some bamboos they are very numerous from the lower nodes of the erect culms, and pass downwards to the soil, whilst those from the upper nodes shrivel up and form circles of spiny fibres.

**Stem.**—The underground stem or rootstock (rhizome) of perennial grasses is usually well developed, and often forms very long creeping or subterranean rhizomes, with elongated internodes and sheathing scales; the widely-creeping, slender rhizomes in Marram-grass (*Ammophila*), *Agropyrum junceum*, *Elymus arenarius*, and other sand-loving plants render them useful as sand-binders. The turf-formation, which is characteristic of open situations in cool temperate climates, results from an extensive production of short stolons, the branches and the fibrous roots developed from their nodes forming the dense “sod.” The rhizome is always solid, and has the usual internal structure of the monocotyledonous stem. In the cases of branching the branches break directly through the sheath of the leaf in connection with which they arise. In other cases the branches grow upwards through the sheaths which they ultimately split from above, and emerging as aerial shoots give a tufted habit to the plant. Good examples are the oat, cock's-foot (*Dactylis*) and other British grasses. This mode of growth is the cause of the “tillering” of cereals, or the production of a large number of erect growing branches from the lower nodes of the young stem. Isolated tufts or tussocks are also characteristic of steppe—and savannah—vegetation and open places generally in the warmer parts of the earth.



The aerial leaf-bearing branches (culms) are a characteristic feature of grasses. They are generally numerous, erect, cylindrical (rarely flattened) and conspicuously jointed, with evident nodes. The nodes are solid, a strong plate of tissue passing across the stem, but the internodes are commonly hollow, although examples of completely solid stems are not uncommon (e.g., maize, many species of *Andropogon*, sugar-cane). The swollen nodes are a characteristic feature. In wheat, barley and most of the British native grasses they are a development, not of the culm, but of the base of the leaf-sheath. The function of the nodes is to raise again stems which have become bent down; they are composed of highly turgescient tissue, the cells of which, under the influence of gravity, elongate on the side next the earth when the culm is placed in a horizontal or oblique position, and thus raise the culm again to an erect position. The internodes continue to grow in length, especially the upper ones, for some time; the increase takes place in a zone at the extreme base, just above the node. The exterior of the culms is more or less concealed by the leaf-sheaths; it is usually smooth and often highly polished, the epidermal cells containing an amount of silica sufficient to leave after burning a distinct skeleton of their structure. *Tabasheer* is a white substance mainly composed of silica, found in the joints of several bamboos. A few of the lower internodes may become enlarged and subglobular, forming nutriment-stores, and grasses so characterized are termed "bulbous" (*Arrhenatherum*, *Poa bulbosa*, etc.). In internal structure grass-culms, save in being hollow, conform to that usual in monocotyledons; the vascular bundles run parallel in the internodes, but a horizontal interlacement occurs at the nodes. In grasses of temperate climates branching is rare at the upper nodes of the culm, but it is characteristic of the bamboos and many tropical grasses. In many bamboos they are long and spreading or drooping and copiously ramified, in others they are reduced to hooked spines. One genus (*Dinochloa*, a native of the Malay archipelago) is scandent, and climbs over trees 100 ft. or more in height. *Olyra latifolia*, a widely-spread tropical species, is also a climber, but on a smaller scale.

Grass-culms grow with great rapidity, as is most strikingly seen in bamboos, where a height of over 100 ft. is attained in from two to three months, and many species grow two, three or even more feet in twenty-four hours.

**Leaves.**—These present special characters usually sufficient for ordinal determination. They are solitary at each node and arranged in two rows, the lower often crowded, forming a basal tuft. They consist of two distinct portions, the sheath and the blade. The sheath is often of great length, and generally completely surrounds the culm, forming a firm protection for the internode, the younger basal portion of which, including the zone of growth, remains tender for some time. As a rule it is split down its whole length, thus differing from that of Cyperaceae which is almost invariably (*Eriospora* is an exception) a complete tube; in some grasses, however (species of *Poa*, *Bromus* and others), the edges are united. The sheaths are much dilated in *Alopecurus vaginatus* and in a species of *Potamochoa*, in the latter, an East Indian aquatic grass, serving as floats. At the summit of the sheath, above the origin of the blade, is the *ligule*, a usually membranous process of small size (occasionally reaching 1 in. in length) erect and pressed around the culm. It is rarely quite absent, but may be represented by a tuft of hairs (very conspicuous in *Pariana*). It serves to prevent rain-water, which has run down the blade, from entering the sheath. *Melica uniflora* has in addition to the ligule, a green erect tongue-like process, from the line of junction of the edges of the sheath.

The blade is frequently wanting or small and imperfect in the basal leaves, but in the rest is long and set on to the sheath at an angle. The usual form is familiar—sessile, more or less ribbon-shaped, tapering to a point, and entire at the edge. The chief modifications are the articulation of the deciduous blade on to the sheath, which occurs in all the Bambuseae (except *Planotia*) and in *Spartina stricta*; and the interposition of a petiole between the sheath and the blade, as in bamboos, *Leptaspis*, *Pharus*, *Pariana*, *Lophatherum* and others. In the latter case the

leaf usually becomes oval, ovate or even cordate or sagittate, but these forms are found in sessile leaves also (*Olyra*, *Panicum*). The venation is strictly parallel, the midrib usually strong, and the other ribs more slender. In *Anomochloa* there are several nearly equal ribs and in some broad-leaved grasses (*Bambuseae*, *Pharus*, *Leptaspis*) the venation becomes tessellated by transverse connecting veins. The tissue is often raised above the veins, forming longitudinal ridges, generally on the upper face; the stomata are in lines in the intervening furrows. The thick prominent veins in *Agropyrum* occupy the whole upper surface of the leaf. Epidermal appendages are rare, the most frequent being marginal, saw-like, cartilaginous teeth, usually minute, but occasionally (*Danthonia scabra*, *Panicum serratum*) so large as to give the margin a serrate appearance. The leaves are occasionally woolly, as in *Alopecurus lanatus* and one or two *Panicums*. The blade is often twisted, frequently so much so that the upper and under faces become reversed. In dry country, e.g., sand dune, the blades of grasses are often folded on the midrib, or rolled up. The rolling is effected by bands of large wedge-shaped cells—motor-cells—between the nerves; the loss of water by these cells as they dry, causes the blade to curl towards the face on which they occur. The rolling up acts as a protection from too great loss of water, the exposed surface being specially protected to this end by a strong cuticle, the majority or all of the stomata occurring on the protected surface. The stiffness of the blade, which becomes very marked in dry-country grasses, is due to the development of girders of thick-walled mechanical tissue which follow the course of all or the principal veins.

**Inflorescence.**—This possesses an exceptional importance in grasses, since, their floral envelopes being much reduced and the sexual organs of very great uniformity, the characters employed for classification are mainly derived from the arrangement of the flowers and their investing bracts. Various interpretations have been given to these glumaceous organs and different terms employed for them by various writers. It may, however, be considered as settled that the whole of the bodies known as glumes and paleae, and arranged externally to the flower, form no part of the floral envelopes, but are of the nature of bracts. These are arranged so as to form *spikelets*, and each spikelet may contain one, as in *Agrostis*, two, as in *Aira*, three, or a great number of flowers, as in *Briza*, *Triticum*; in some species of *Eragrostis* there are nearly 60. The flowers are, as a rule, placed laterally on the axis (*rachilla*) of the spikelet, but in one-flowered spikelets they appear to be terminal, and are probably really so in *Anthoxanthum* and in two anomalous genera, *Anomochloa* and *Streptochaeta*.

In immediate relation with the flower itself, and often entirely concealing it, is the *palea* or *pale* ("upper pale" of most systematists). This organ is peculiar to grasses among Glumiflorae (the series to which belong the two families Gramineae and Cyperaceae), and is almost always present, certain *Oryzeae* and *Phalarideae* being the only exceptions. It is of thin membranous consistence, usually obtuse, often bifid, and possesses no central rib or nerve, but has two lateral ones, one on either side; the margins are frequently folded in at the ribs, which thus become placed at the sharp angles. The pale is generally considered to represent a single bracteole, characteristic of Monocotyledons, the binerved structure being the result of the pressure of the axis of the spikelet during the development of the pale, as in *Iris* and others.

The flower with its pale is sessile, and is placed in the axil of another bract in such a way that the pale is exactly opposed to it, though at a slightly higher level. It is this second bract or flowering glume which has been generally called by systematists the "lower pale," and with the "upper pale" was formerly considered to form an outer floral envelope. The two bracts are, however, on different axes, one secondary to the other, and cannot therefore be parts of one whorl of organs. They are usually quite unlike one another, but in some genera (e.g., most *Festuceae*) are very similar in shape and appearance.

The flowering glume has generally a more or less boat-shaped form, is of firm consistence, and possesses a well-marked central



midrib and frequently several lateral ones. The midrib in a large proportion of genera extends into an appendage termed the *awn*, and the lateral veins more rarely extend beyond the glume as sharp points (e.g., *Pappophorum*). The form of the flowering glume is very various, this organ being plastic and extensively modified in different genera. It frequently extends downwards a little on the rachilla; in *Leptaspis* it is formed into a closed cavity by the union of its edges, and encloses the flower, two styles projecting through the pervious summit. Valuable characters for distinguishing genera are shown from the awn. This presents itself variously developed from a meresubulate point to an organ several inches in length, and when complete (as in *Andropogoneae*, *Aveneae* and *Stipeae*) consists of two well-marked portions, a lower twisted part and a terminal straight portion, usually set in at an angle with the former, sometimes trifid and occasionally beautifully feathery. The lower part is most often suppressed, and in the large group of the *Paniceae* awns of any sort are very rarely seen. The awn may be either terminal or may come off from the back of the flowering glume. When terminal the awn has three fibro-vascular bundles, when dorsal only one; it is covered with the stomate-bearing epidermis.

The flower with its palea is thus sessile in the axil of a floriferous glume, and in a few grasses (*Leersia*, *Coleanthus*, *Nardus*) the spikelet consists of nothing more, but usually (even in uniflorous spikelets) other glumes are present. Of these the two placed distichously opposite each other at the base of the spikelet never bear any flower in their axils, and are known as the *empty* or *barren glumes*. They are the "glumes" of most writers. They very rarely differ much from one another, but one may be smaller or quite absent (*Panicum*, *Setaria*, *Paspalum*, *Lolium*), or both be altogether suppressed, as above noticed. They are commonly firm and strong, often enclose the spikelet, and are rarely provided with long points or imperfect awns. Generally speaking they do not share in the special modifications of the flowering glumes, and rarely themselves undergo modification, chiefly in hardening of portions (*Sclerachne*, *Manisuris*, *Anthe-phora*, *Peltophorum*), so as to afford greater protection to the flowers or fruit. But it is usual to find, besides the basal glumes, a few other empty ones, and these are in two- or more-flowered spikelets (*Triticum*) at the top of the rachilla (numerous in *Lophatherum*), or in uniflorous ones below and interposed between the floral glume and the basal pair.

The axis of the spikelet is frequently jointed and breaks up into articulations above each flower. Tufts or borders of hairs are frequently present (*Calamagrostis*, *Phragmites*, *Andropogon*), and are often so long as to surround and conceal the flowers. The axis is often continued beyond the last flower or glume as a bristle or stalk.

*Involucres* or organs outside the spikelets also occur and are formed in various ways. Thus in *Setaria*, *Pennisetum*, etc., the one or more circles of simple or feathery hairs represent abortive branches of the inflorescence; in *Cenchrus* these become consolidated, and the inner ones are flattened so as to form a very hard globular spiny case to the spikelets. Bracts of a more general character subtending branches of the inflorescence are singularly rare in Gramineae, in marked contrast with Cyperaceae, where they are so conspicuous. The remarkable ovoid involucre of *Coix*, which becomes of stony hardness, white and polished (then known as "Job's tears," *q.v.*), is also a modified bract or leaf-sheath.

Any number of spikelets may compose the inflorescence, and their arrangement is very various. In the spicate forms, with sessile spikelets on the main axis, the latter is often dilated and flattened (*Paspalum*), or is more or less thickened and hollowed out (*Stenotaphrum*, *Rottboellia*, *Tripsacum*), when the spikelets are sunk and buried within the cavities. Every variety of racemose and paniculate inflorescence obtains, and the number of spikelets composing those of the large kinds is often immense. Rarely the inflorescence consists of very few flowers; thus *Lygeum* *Spartum*, one of the esparto grasses and the most anomalous of European grasses, has but two or three large uniflorous spikelets, which are fused together at the base, and have no basal glumes,

but are enveloped in a large, hooded, spathe-like bract.

*Flower*.—This is characterized by remarkable uniformity. The perianth is represented by very rudimentary, small, fleshy scales arising below the ovary, called *lodicules*; they are elongated or truncate, are sometimes fringed with hairs, and are in contact with the ovary. Their usual number is two, and they are placed collaterally at the anterior side of the flower, that is, within the flowering glume. They are generally considered to represent the inner whorl of the ordinary monocotyledonous (liliaceous) perianth, the outer whorl of these being suppressed as well as the posterior member of the inner whorl. This latter is present almost constantly in *Stipeae* and *Bambuseae*, which have three lodicules, and in the latter group they are occasionally more numerous. In *Streptochaeta* there are six lodicules, alternately arranged in two whorls. Sometimes, as in *Anthoxanthum*, they are absent. In *Melica* there is one large anterior lodicule resulting presumably from the union of the two which are present in allied genera. The function of the lodicules is the separation of the pale and glume to allow the protrusion of stamens and stigmas; they effect this by swelling and thus exerting pressure on the base of these two structures. Where, as in *Anthoxanthum*, there are no lodicules, pale and glume do not become laterally separated, and the stamens and stigmas protrude only at the apex of the floret. Grass-flowers are usually hermaphrodite, but there are very many exceptions. Thus it is common to find one or more imperfect (usually male) flowers in the same spikelet with bisexual ones, and their relative position is important in classification. *Holcus* and *Arrhenatherum* are examples in English grasses; and as a rule in species of temperate regions separation of the sexes is not carried further. In warmer countries monoecious and dioecious grasses are most frequent. In such cases the male and female spikelets and inflorescence may be very dissimilar, as in maize, Job's tears, *Euchlaena*, *Spinifex*, etc.; and in some dioecious species this dissimilarity has led to the two sexes being referred to different genera. In other grasses, however, with the sexes in different plants (e.g., *Brizopyrum*, *Distichlis*, *Eragrostis capitata*, *Gynerium*), no such dimorphism obtains. *Amphicarpum* is remarkable in having cleistogamic flowers borne on long radical subterranean peduncles which are fertile, whilst the conspicuous upper paniculate ones, though apparently perfect, never produce fruit. Something similar occurs in *Leersia oryzoides*, where the fertile spikelets are concealed within the leaf-sheaths.

*Androecium*.—In the vast majority there are three stamens alternating with the lodicules, and therefore one anterior, *i.e.*, opposite the flowering glume, the other two being posterior and in contact with the palea. They are hypogynous, and have long and very delicate filaments, and large, linear or oblong two-celled anthers, dorsifixed and ultimately very versatile, deeply indented at each end, and commonly exserted and pendulous. Suppression of the anterior stamen sometimes occurs, or the two posterior ones may be absent. There is in some genera (*Oryza*, most *Bambuseae*) another row of three stamens, making six in all. The stamens become numerous (ten to forty) in the male flowers of a few monoecious genera (*Pariana*, *Luziola*). In *Ochlandra* they vary from seven to thirty, and in *Gigantochloa* they are monadelphous.

*Gynoecium*.—The pistil consists of a single carpel, opposite the pale in the median plane of the spikelet. The ovary is small, rounded to elliptical, and one-celled, and contains a single slightly bent ovule sessile on the ventral suture (that is, springing from the back of the ovary); the micropyle points downwards. It bears usually two lateral styles which are quite distinct or connate at the base, sometimes for a greater length; each ends in a densely hairy or feathery stigma. Occasionally there is but a single style, as in *Nardus*, which corresponds to the midrib of the carpel. The very long and apparently simple stigma of maize arises from the union of two. Many of the bamboos have a third, anterior, style.

Comparing the flower of Gramineae with the general monocotyledonous plan as represented by Liliaceae and other families, it will be seen to differ in the absence of the outer row and



the posterior member of the inner row of the perianth-leaves, of the whole inner row of stamens, and of the two lateral carpels, whilst the remaining members of the perianth are in a rudimentary condition. But each or any of the usually missing organs are to be found normally in different genera, or as occasional developments.

**Pollination and Germination.**—Grasses are generally wind-pollinated, though self-fertilization occurs. A few species, as we have seen, are monoecious or dioecious, while many are polygamous (having unisexual as well as bisexual flowers as found in many members of the tribes *Andropogoneae* and *Paniceae*), and in these the male flower of a spikelet always blooms later than the hermaphrodite, so that its pollen can only effect cross-fertilization upon other spikelets in the same or another plant. Of those with only bisexual flowers, many are strongly protogynous (the stigmas protruding before the anthers are ripe), such as *Alopecurus* and *Anthoxanthum*, but generally the anthers protrude first and discharge the greater part of their pollen before the stigmas appear. The filaments elongate rapidly at flowering-time, and the lightly versatile anthers empty an abundance of finely granular, smooth pollen through a longitudinal slit. Some flowers, such as rye, have lost the power of effective self-fertilization, but in most cases both forms, self- and cross-fertilization, seem to be possible. Thus the species of wheat are usually self-fertilized, but cross-fertilization is possible since the glumes are open above, the stigmas project laterally, and the anthers empty only about one-third of their pollen in their own flower and the rest into the air. In some cultivated races of barley, cross-fertilization is precluded, as the flowers never open.

**Fruit and Seed.**—The ovary ripens into a usually small ovoid or rounded fruit, which is entirely occupied by the single large seed, from which it is not to be distinguished, the thin pericarp of the fruit being completely united to the testa of the seed. To this peculiar fruit the term *caryopsis* has been applied (more familiarly "grain"); it is commonly furrowed longitudinally down one side (usually the inner, but in *Coix* and its allies, the outer), and an additional covering is not unfrequently provided by the adherence of the persistent palea, or even also of the flowering glume ("chaff" of cereals). From this type there are a few deviations; thus in *Sporobolus*, etc., the pericarp is not united with the seed but is quite distinct, dehisces, and allows the loose seed to escape. Sometimes the pericarp is hard, forming a nut, as in some genera of *Bambuseae*, while in other *Bambuseae* it becomes thick and fleshy, forming a berry often as large as an apple. In *Melocanna* the berry forms an edible fruit 3 or 4 in. long, with a pointed beak of 2 in. more; it is indehiscent, and the small seed germinates whilst the fruit is still attached to the tree, putting out a tuft of roots and a shoot, and not falling till the latter is 6 in. long. The position of the embryo is plainly visible on the front side at the base of the grain. On the other, posterior, side of the grain is a more or less evident, sometimes punctiform, sometimes elongated or linear mark, the hilum, the place where the ovule was fastened to the wall of the ovary. The form of the hilum is constant throughout a genus, and sometimes also in whole tribes.

The testa is thin and membranous but occasionally coloured, and the embryo small, the great bulk of the seed being occupied by the hard farinaceous endosperm (albumen) on which the nutritive value of the grain depends. The outermost layer of endosperm, the aleurone-layer, consists of regular cells filled with small proteid granules; the rest is made up of large polygonal cells containing numerous starch-grains in a matrix of proteid which may be continuous (horny endosperm) or granular (mealy endosperm). The embryo presents many points of interest. Its position is remarkable, closely applied to the surface of the endosperm at the base of its outer side. This character is absolute for the whole order, and effectually separates Gramineae from Cyperaceae. The part in contact with the endosperm is plate-like, and is known as the *scutellum*; the surface in contact with the endosperm shows a special epithelial layer concerned in absorption of materials from the endosperm. In some grasses there is a small scale-like appendage opposite the scutellum, the

*epiblast*. Three structures have been claimed as representing the cotyledon:—(1) the scutellum, connected by vascular tissue with the vascular cylinder of the main axis of the embryo which it more or less envelops; (2) the cellular outgrowth of the axis, the epiblast, small and inconspicuous as in wheat, or larger as in *Stipa*; (3) the coleoptile or germ-sheath, arising on the same side of the axis and above the scutellum, enveloping the plumule in the seed and appearing above ground as a generally colourless sheath from the apex of which the plumule ultimately breaks. The development of these structures, especially in relation to the origin of the vascular bundles which supply them, favours the view that the scutellum and coleoptile are highly differentiated parts of a single cotyledon.

**Germination.**—In germination the coleorhiza lengthens, ruptures the pericarp and fixes the grain to the ground by developing numerous hairs. The radicle then breaks through the coleorhiza, as do also the secondary rootlets where, as in the case of many cereals, these have been formed in the embryo. The germ-sheath grows vertically upwards, its stiff apex pushing through the soil, while the plumule is hidden in its hollow interior. Finally the plumule escapes, its leaves successively breaking through at the tip of the coleoptile. The scutellum meanwhile feeds the developing embryo by absorbing from the endosperm. The growth of the primary root is limited; sooner or later adventitious roots develop from the axis above the radicle which they ultimately exceed in growth.

**Means of Distribution.**—Various methods of scattering the grain have been adopted, in which parts of the spikelet or inflorescence are concerned. Short spikes may fall from the culm as a whole; or the axis of a spike or raceme is jointed so that one spikelet falls with each joint as in many *Andropogoneae* and *Hordeae*. In many-flowered spikelets the rachilla is often jointed and breaks into as many pieces as there are fruits, each piece bearing a glume and pale. These arrangements are, with few exceptions, lacking in cultivated cereals though present in their wild forms, so far as these are known. Such arrangements are disadvantageous for the complete gathering of the fruit, and therefore varieties in which they are not present would be preferred for cultivation. The persistent bracts (glume and pale) afford an additional protection to the fruit; they protect the embryo, which is near the surface, from too rapid wetting and, when once soaked, from drying up again. They also decrease the specific gravity, so that the grain is more readily carried by the wind, especially when, as in *Briza*, the glume has a large surface compared with the size of the grain, or when, as in *Holcus*, empty glumes also take part; in Canary grass (*Phalaris*) the large empty glumes bear a membranous wing on the keel.

The awn which is frequently borne on the flowering glume is also a very efficient means of distribution, catching into fur of animals or plumage of birds, or as often in *Stipa* forming a long feather for wind-carriage. In *Tragus* the glumes bear numerous short hooked bristles. The fleshy berries of some *Bambuseae* favour distribution by animals.

The awn is also of use in burying the fruit in the soil. Thus in *Stipa*, species of *Avena*, *Heteropogon* and others the base of the glume forms a sharp point which will easily penetrate the ground; above the point are short stiff upwardly pointing hairs which oppose its withdrawal. The long awn, which is bent and closely twisted below the bend, acts as a driving organ; it is very hygroscopic, the coils untwisting when damp and twisting up when dry. The repeated twisting and untwisting, especially when the upper part of the awn has become fixed in the earth or caught in surrounding vegetation, drives the point deeper and deeper into the ground. Such grasses often cause harm to sheep by catching in the wool and boring through the skin.

A peculiar method of distribution occurs in some alpine and arctic grasses, which grow under conditions where ripening of the fruit is often uncertain. The entire spikelet, or single flowers, are transformed into small-leaved shoots which fall from the axes and readily root in the ground. Some species, such as *Poa stricta*, are known only in this *viviparous* condition; others, like our British species *Festuca ovina* and *Poa alpina*, become *vivi-*



parous under the special climatic conditions.

**Classification.**—Gramineae are sharply defined from all other plants. The only family closely allied is Cyperaceae, and the points of difference between the two may be here brought together. The best distinctions are found in the position of the embryo in relation to the endosperm—lateral in grasses, basal in Cyperaceae—and in the possession by Gramineae of the 2-nerved palea below each flower. Less absolute characters, but generally trustworthy and more easily observed, are the feathery stigmas, the always distichous arrangement of the glumes, the usual absence of more general bracts in the inflorescence, the split leaf-sheaths, and the hollow, cylindrical, jointed culms—some or all of which are wanting in all Cyperaceae. The same characters will distinguish grasses from the other glumiferous orders, Restiaceae, and Eriocaulonaceae, which are besides further removed by their capsular fruit and pendulous ovules. To other monocotyledonous families the resemblances are merely of adaptive or vegetative characters. Some Commelinaceae and Marantaceae approach grasses in foliage; the leaves of *Allium*, etc., possess a ligule; the habit of some palms reminds one of the bamboos; and Juncaceae and a few Liliaceae possess an inconspicuous scarious perianth. There are about 450 genera containing about 4,500 well-defined species. About 100 species, grouped in 42 genera, occur in Great Britain. According to A. S. Hitchcock about 1,500 species, grouped in 144 genera, are found in the United States.

The great uniformity among the very numerous species of this vast family renders its *classification* very difficult. The difficulty has been increased by the confusion resulting from the multiplication of genera founded on slight characters, and from the description (in consequence of their wide distribution) of identical plants under several different genera.

No characters for main divisions can be obtained from the flower proper or fruit (with the exception of the character of the hilum), and it has therefore been found necessary to trust to characters derived from the usually less important inflorescence and bracts.

The following arrangement has been proposed by Professor Eduard Hackel in his monograph on the order.

A. Spikelets one-flowered, rarely two-flowered as in *Zea*, falling from the pedicel entire or with certain joints of the rachis at maturity. Rachilla not produced beyond the flowers.

a. Hilum a point; spikelets not laterally compressed.

α Fertile glume and pale hyaline; empty glumes thick, membranous to coriaceous or cartilaginous, the lowest the largest. Rachis generally jointed and breaking up when mature.

1. Spikelets unisexual, male and female in separate inflorescences or on different parts of the same inflorescence. 1. *Maydeae*.

2. Spikelets bisexual, or male and bisexual, each male standing close to a bisexual. 2. *Andropogoneae*.

β Fertile glume and pale cartilaginous, coriaceous or papery; empty glumes more delicate, usually herbaceous, the lowest usually smallest, Spikelets falling singly from the unjointed rachis of the spike or the ultimate branches of the panicle.

3. *Paniceae*.

b. Hilum a line; spikelets laterally compressed.

4. *Oryzeae*.

B. Spikelets one- to indefinite-flowered; in the one-flowered the rachilla frequently produced beyond the flower; rachilla generally jointed above the empty glumes, which remain after the fruiting glumes have fallen. When more than one-flowered, distinct internodes are developed between the flowers.

a. Culm herbaceous annual; leaf-blade sessile, and not jointed to the sheath.

α Spikelets upon distinct pedicels and arranged in panicles or racemes.

I. Spikelets one-flowered.

i. Empty glumes 4.

5. *Phalarideae*.

ii. Empty glumes 2.

6. *Agrostideae*.

II. Spikelets more than one-flowered.

i. Fertile glumes generally shorter than the empty glumes, usually with a bent awn on the back.

7. *Aveneae*.

ii. Fertile glumes generally longer than the empty, unawned or with a straight, terminal awn.

9. *Festuceae*.

β Spikelets crowded in two close rows, forming a one-sided spike or raceme with a continuous (not jointed) rachis.

8. *Chlorideae*.

γ Spikelets in two opposite rows forming an equal-sided spike.

10. *Hordeae*.

b. Culm woody, at any rate at the base, leaf-blade jointed to the sheath, often with a short, slender petiole.

11. *Bambuseae*.

Tribe 1. *Maydeae*. *Zea Mays* (maize, q.v., or Indian corn. *Tripsacum*, 2 or 3 species in subtropical America north of the equator; *Tr. dactyloides* (gama grass) extends northwards to Illinois and Connecticut; it is used for fodder and as an ornamental plant. *Coix Lacryma-Jobi* (Job's tears) q.v.

Tribe 2. *Andropogoneae* (mainly tropical). The spikelets are arranged in spike-like racemes, and generally in pairs consisting of a sessile and stalked spikelet at each joint of the rachis. Many are savannah grasses, in various parts of the tropics, for instance the large genus *Andropogon*, *Elionurus* and others. *Saccharum officinarum* (sugar-cane). *Sorghum*, an important tropical cereal known as black millet or *durra* (q.v.). *Imperata* is a widespread tropical genus; one species *I. arundinacea* is the principal grass of the alang-alang fields in the Malay Archipelago; it is used for thatch. *Vossia*, an aquatic grass, often floating, is found in western India and tropical Africa. In the swampy lands of the upper Nile it forms, along with a species of *Saccharum*, huge floating grass barriers. In *Andropogon Nardus*, a native of India, but also cultivated, the rhizome, leaves and especially the spikelets of which contain a volatile oil, which on distillation yields the citronella oil of commerce. A closely allied species, *A. Schoenanthus* (lemon-grass), yields lemon-grass oil; a variety is used by the negroes in western Africa for haemorrhage. *Themeda Forskalii*, which occurs from the Mediterranean region to South Africa and Tasmania, is the kangaroo grass of Australia, where, as in South Africa, it often covers wide tracts.

Tribe 3. *Paniceae* (tropical to subtropical; a few temperate), a second flower, generally male, rarely hermaphrodite, is often present below the fertile flower. *Paspalum* is a large tropical genus, most abundant in America, especially on the pampas and campos; many species are good forage plants, and the grain is sometimes used for food. *Panicum*, a very polymorphic genus, and one of the largest in the order, is widely spread in all warm countries; together with species of *Paspalum* they form good forage grasses in the South American savannahs and campos. *Panicum Crus-galli* is a polymorphic cosmopolitan grass, which is often grown for fodder; in one form (*P. frumentaceum*) it is cultivated in India for its grain. *P. miliaceum* is millet (q.v.), and *P. altissimum*, Guinea grass. *Digitaria sanguinalis* is a very widespread grass, in Bohemia it is cultivated as a food-grain; it is also the crab-grass of the southern United States, where it is used for fodder.

*Setaria italica*, Hungarian grass, is extensively grown as a food-grain both in China and Japan, parts of India and western Asia, as well as in Europe, where its culture dates from pre-historic times; it is found in considerable quantity in the lake dwellings of the Stone age.

In *Cenchrus* the bristles unite to form a tough spiny capsule; *C. tribuloides* (bur-grass) and other species are troublesome weeds in North and South America, as the involucre clings to the wool of sheep and is removed with great difficulty. *Pennisetum typhoideum* is widely cultivated as a grain in tropical Africa. *Spinifex*, a dioecious grass, is widespread on the coasts of Australia and eastern Asia, forming an important sand-binder. The female heads are spinose with long bracts, fall entire when ripe and are carried away by wind or sea, becoming finally anchored in



the sand and falling to pieces.

Tribe 4. *Oryzeae* (mainly tropical and subtropical). The spikelets are sometimes unisexual, and there are often six stamens. *Leersia* is a genus of swamp grasses, one of which *L. oryzoides* occurs in the north temperate zone of both old and new worlds, and is a rare grass in Surrey, Sussex and Hampshire. *Zizania aquatica* (Tuscarora or Indian rice) is a reed-like grass growing over large areas on banks of streams and lakes in North America and north-east Asia. The Indians collect the grain, *Oryza sativa* (rice, *q.v.*), for food. *Lygeum Spartum*, with a creeping stem and stiff rush-like leaves, is common on rocky soil on the high plains bordering the western Mediterranean, and is one of the sources of esparto.

Tribe 5. *Phalarideae* (a few are South African and Australasian; the others are more widely distributed, and represented in the British flora). *Phalaris arundinacea*, is a reed-grass found on the banks of British rivers and lakes; a variety with striped leaves known as ribbon-grass is grown for ornament. *P. canariensis* (Canary grass, a native of southern Europe and the Mediterranean area) is grown for bird-food and sometimes as a cereal. *Anthoxanthum odoratum*, the sweet vernal grass of our flora, owes its scent to the presence of coumarin, which is also present in the closely allied genus *Hierochloa*, which occurs throughout the temperate and frigid zones.

Tribe 6. *Agrostideae* (occurring in all parts of the world; a number are British). *Aristida* and *Stipa* are large and widely distributed genera, occurring especially on open plains and steppes; the conspicuously awned persistent flowering glume forms an efficient means of dispersing the grain. *Stipa pennata* is a characteristic species of the Russian steppes. *St. spartea* (porcupine grass) and other species are plentiful on the North American prairies. *St. tenacissima* is the Spanish esparto grass (*q.v.*), known in North Africa as halfa or alfa. *Phleum pratense* (timothy) is a valuable fodder grass, as also is *Alopecurus pratensis* (foxtail). *Sporobolus*, a large genus in the warmer parts of both hemispheres, but chiefly America, derives its name from the fact that the seed is ultimately expelled from the fruit. *Agrostis* is a large world-wide genus, but especially developed in the north temperate zone, where it includes important meadow-grasses. *Ammophila arundinacea* (*Psamma arenaria*) (Marram grass) with its long creeping stems forms a useful sand-binder on the coasts of Europe, North Africa and the Atlantic states of America.

Tribe 7. *Aveneae* (seven genera are British). *Holcus lanatus* (Yorkshire fog, soft grass) is a common meadow and wayside grass with woolly or downy leaves. *Aira* is a genus of delicate annuals with slender hair-like branches of the panicle. *Deschampsia* and *Trisetum* occur in temperate and cold regions or on high mountains in the tropics; *T. pratense* (*Avena flavescens*) with a loose panicle and yellow shining spikelets is a valuable fodder-grass. *Avena fatua* is the wild oat and *A. sativa* the cultivated oat (*q.v.*). *Arrhenatherum avenaceum*, a perennial field grass, native in Britain and central and southern Europe, is cultivated in North America.

Tribe 8. *Chlorideae* (chiefly in warm countries). The only British representative is *Cynodon Dactylon* (dog's tooth, Bermuda grass) found on sandy shores in the south-west of England; it is a cosmopolitan, covering the ground in sandy soils, and forming an important forage grass in many dry climates (Bermuda grass of the southern United States, and known as durba, dub and other names in India). Species of *Chloris* are grown as ornamental grasses. *Bouteloua* with numerous species (mesquite grass, grama grass) on the plains of the south-western United States, afford good grazing. *Eleusine indica* is a common tropical weed; the nearly allied species *E. coracana* is a cultivated grain in the warmer parts of Asia and throughout Africa. *Buchloe dactyloides* is the buffalo grass of the North American prairies, a valuable fodder.

Tribe 9. *Festuceae* (tropical, temperate, arctic and alpine forms). Many are important meadow-grasses; 15 are British. *Gynierium argenteum* (pampas grass) is a native of southern Brazil and Argentina. *Arundo* and *Phragmites* are tall reed-

grasses (*see* REED). Several species of *Triodia* cover large areas of the interior of Australia, and from their stiff, sharply pointed leaves are very troublesome. *Eragrostis*, one of the larger genera of the order, is widely distributed in the warmer parts of the earth; many species are grown for ornament and *E. abyssinica* is an important food-plant in Abyssinia. *Koeleria cristata* is a fodder-grass. *Briza media* (quaking grass) is a useful meadow-grass. *Dactylis glomerata* (cock's-foot), a perennial grass with a dense panicle, common in pastures and waste places, is a useful meadow-grass. It has become naturalized in North America, where it is known as orchard grass, as it will grow in shade. *Cynosurus cristatus* (dog's tail) is a common pasture-grass. *Poa*, a large genus widely distributed in temperate and cold countries, includes many meadow and alpine grasses; eight species are British; *P. annua* is the very common weed in paths and waste places; *P. pratensis* and *P. trivialis* are also common grasses of meadows, banks and pastures, the former is the "June grass" or "Kentucky blue grass" of North America; *P. alpina* is a mountain grass of the northern hemisphere and found also in the Arctic region. The largest species of the genus is *Poa flabellata* which forms great tufts 6-7 ft. high with leaves arranged like a fan. *Glyceria fluitans*, manna-grass, so-called from the sweet grain, is one of the best fodder grasses for swampy meadows; the grain is an article of food in central Europe. *Festuca* (fescue) is also a large and widely distributed genus, but found especially in the temperate and cold zones; it includes valuable pasture grasses, such as *F. ovina* (sheep's fescue), *F. rubra*; nine species are British. The closely allied genus *Bromus* (brome grass) is also widely distributed but most abundant in the north temperate zone; *B. erectus* is a useful forage grass on dry chalky soil.

Tribe 10. *Hordeae* (about 19 genera, widely distributed; six are British). *Nardus stricta* (mat-weed), found on heaths and dry pastures, is a small perennial useless grass with slender rigid stem and leaves. *Lolium perenne*, ray- (or by corruption rye-) grass, is common in waste places and a valuable pasture-grass; *L. italicum* is the Italian ray-grass; *L. temulentum* (darnel) has many of its grains infected with a fungus which is passed on from generation to generation. *Secale cereale*, rye (*q.v.*), is cultivated mainly in northern Europe. *Agropyrum repens* (couch grass) has a long creeping underground stem, and is a troublesome weed in cultivated land; the widely creeping stem of *A. junceum*, found on sandy sea-shores, renders it a useful sand-binder. *Triticum sativum* is wheat (*q.v.*), and *Hordeum sativum*, barley (*q.v.*). *H. murinum*, wild barley, is a common grass in waste places. *Elymus arenarius* (lyme grass) occurs on sandy sea-shores in the north temperate zone and is a useful sand-binder.

Tribe 11. *Bambuseae*. Contains 23 genera, mainly tropical. *See* BAMBOO.

**Distribution.**—Grasses are the most universally diffused of all flowering plants. There is no district in which they do not occur, and in nearly all they are a leading feature of the flora. In number of species Gramineae comes considerably below Compositae and Leguminosae, the two most numerous orders of phanerogams, but in number of individual plants it probably far exceeds either; whilst from the wide extension of many of its species, the proportion of Gramineae to other orders in the various floras of the world is much higher than its number of species would lead one to expect. In tropical regions, where Leguminosae is the leading order, grasses closely follow as the second, whilst in the warm and temperate regions of the northern hemisphere, in which Compositae takes the lead, Gramineae again occupies the second position.

While the greatest number of species is found in the tropical zone, the number of individuals is greater in the temperate zones, where they form extended areas of turf. Turf- or meadow-formation depends upon uniform rainfall. Grasses also characterize steppes and savannahs, where they form scattered tufts. The bamboos are a feature of tropical forest vegetation, especially in the monsoon region. As the colder latitudes are entered the grasses become relatively more numerous, and are the leading family in Arctic and Antarctic regions. The only countries where the order plays a distinctly subordinate part are some extra-tropical regions



of the southern hemisphere, Australia, the Cape, Chile, etc. The proportion of graminaceous species to the whole phanerogamic flora in different countries varies from nearly  $\frac{1}{4}$  in the Arctic regions to about  $\frac{1}{25}$  at the Cape; in the British Isles it is about  $\frac{1}{12}$ .

The principal climatic cause influencing the number of graminaceous species appears to be amount of moisture. A remarkable feature of the distribution of grasses is its uniformity; there are no great centres for the order, as in Compositae, where a marked preponderance of endemic species exists; and the genera, except some of the smallest or monotypic ones, have usually a wide distribution.

Many grasses are almost cosmopolitan, such as the common reed, *Phragmites communis*; and many range throughout the warm regions of the globe, e.g., *Cynodon Dactylon*, *Eleusine indica*, *Imperata arundinacea*, *Sporobolus indicus*, etc., and such weeds of cultivation as species of *Setaria*, *Echinochloa*. Several species of the north temperate zone, such as *Poa nemoralis*, *P. pratensis*, *Festuca ovina*, *F. rubra* and others are absent in the tropics but reappear in the Antarctic regions; others (e.g., *Phleum alpinum*) appear in isolated positions on high mountains in the intervening tropics. No tribe is confined to any one hemisphere and no large genus to any one floral region; facts which clearly indicate that the separation of the different tribes goes back to very ancient times.

Of specially remarkable species *Lygeum* is found on the seashore of the eastern half of the Mediterranean basin, and the minute *Coleanthus* occurs in three or four isolated spots in Europe (Norway, Bohemia, Austria, Normandy), in North-east Asia (Amur) and on the Pacific coast of North America (Oregon, Washington). Many remarkable endemic genera occur in tropical America, including *Anomochloa* of Brazil, and most of the large aquatic species with separated sexes are found in this region. The only genus of flowering plants peculiar to the Arctic regions is the beautiful and rare grass *Pleuropogon Sabinii*, of Melville Island.

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**BLOOM**, the blossom of flowering plants or the powdery film on the skin of fresh-picked fruit.

**BOLL**, a botanical term for a fruit-pod, particularly of the cotton plant.

**CAPSULE**, a term in botany for a dry seed vessel, as in the poppy, iris, foxglove, etc., with one or more cavities. When ripe the capsule opens and scatters the seed (see **FRUIT**).

**CACTUS**. This word, applied by the ancient Greeks to some prickly plant, was adopted by Linnaeus as the name of a group of curious succulent or fleshy-stemmed plants, most of them prickly and leafless, some of which produce beautiful flowers, and are now popular in gardens. As applied by Linnaeus, the name *Cactus* is almost conterminous with what is now the family *Cactaceae*.

The *Cacti* may be described in general terms as plants having a woody axis, or skeleton, overlaid with thick masses of cellular tissue forming the fleshy stems. These are extremely various in character and form, being globose, cylindrical, columnar or flattened into leafy expansions of thick joint-like divisions, the surface being either ribbed like a melon, or developed into nipple-like protuberances, or variously angular, or smooth, but in the greater number of species furnished copiously with tufts of horny spines, some of which are exceedingly keen and powerful. These tufts show the position of buds, of which, however, comparatively few are developed. The leaves, if present, are generally much reduced. In *Pereskia*, however, the stems are less succulent, and the leaves, though fleshy, are developed in the usual form. The flowers are frequently large and showy, and are often attractive from their

high colouring. In one group, represented by *Cereus* and related genera, they consist of a tube, elongated, on the outer surface of which, towards the base, are developed small and at first inconspicuous scales, which gradually increase in size upwards and at length become crowded, numerous and petaloid, forming a funnel-shaped blossom, the beauty of which is much enhanced by the multitude of conspicuous stamens which with the pistil occupy



FIG. 1.—CACTUS FENCES IN SOUTHERN MEXICO

the centre. In another group, represented by *Opuntia*, the flowers are rotate; i.e., the long tube is replaced by a very short one. At the base of the tube, in both groups, the ovary develops into a fleshy (often edible) fruit, that produced by the *Opuntias* being known as the prickly pear or Indian fig.

Genera with long-tubed flowers include *Echinocactus*, *Echinopsis*, *Cereus*, *Epiphyllum*, *Cephalocereus* and many others, while



FIG. 2.—PRICKLY PEAR CACTUS

The illustration shows the flattened branch of swollen stem which stores up water and spiny leaves which reduce transpiration

those with short-tubed flowers are *Rhipsalis*, *Opuntia*, *Pereskia* and several of minor importance. *Cactaceae* belong to the New World; but some of the *Opuntias* have been long distributed on the shores of the Mediterranean and the volcanic soil of Italy and several species of *Rhipsalis* occur in tropical Asia and Africa. They mostly affect the hot, dry regions of tropical America, the aridity of which they are enabled to withstand in consequence of the thickness of their cuticle and the fewness and "sunk" condition of the stomata with which they are furnished. The thick



fleshy stems and branches contain a store of water. The succulent fruits of some kinds are not only edible but agreeable, and in fevers are freely administered as a cooling drink. The Spanish-Americans plant the *Opuntias* and others around their houses, where they serve as impenetrable fences.

CACTUS (fig. 1), the genus of melon-thistle or Turk's cap cactuses, contains about 18 species, which are found in the West Indies, Mexico, Venezuela and Colombia. The typical species, *Cactus melocactus*, of Jamaica, forms a succulent mass of ovoid form, from 1 to 2 ft. high, the surface divided into numerous furrows like the ribs of a melon, with projecting angles, which are set with a regular series of stellated spines—each bundle consisting of about five larger spines, accompanied by smaller but sharp bristles—and the top of the plant being surmounted by a cylindrical crown 3 to 5 in. high, composed of reddish-brown, needle-like bristles, closely packed with cottony wool. At the summit of this crown the small rosy-pink flowers are produced, half protruding from the mass of wool, and these are succeeded by small red or pink, elongated berries. These plants usually grow in rocky places with little or no earth to support them. The fruit of this and related species, which has an agreeably acid flavour, is eaten in the West Indies. The group is distinguished by the distinct *cephalum* or crown which bears the flowers. *Disocactus*, a related genus, consists of about 7 species native to Brazil and Paraguay.

ECHINOCACTUS (fig. 3) is the genus bearing the popular name of hedgehog cactus. It comprises nine species, native of the southwestern United States and Mexico. They have the fleshy stems characteristic of the family, these being either globose, oblong or cylindrical, and ribbed as in *Melocactus*, and armed with stiff sharp spines, set in little woolly cushions occupying the place of the buds. The flowers, produced near the top of the plant, are large and showy, yellow and rose being the prevailing colours. They are succeeded by succulent fruits, which are exserted, and scaly, in which respects this genus differs from *Melocactus* which has the fruits partly immersed and smooth. One of the most interesting species is *E. ingens*, in which there are 40 to 50 ridges, on which the buds and clusters of spines are sunk at intervals, the aggregate number of the spines having been in some cases computed at 50,000 on one plant. There are 27 related genera.

CEREUS.—This genus bears the common name of torch thistle. It comprises about 25 species, largely Mexican but scattered through South America and the West Indies. The stems are columnar or elongated, some of the latter creeping on the ground. There are many related genera. *Carnegiea gigantea*, the largest of all cacti, is a native to hot, arid, desert regions of the southwestern United States, growing in rocky valleys and on mountain sides. The stems grow to a height of 70 ft. and have a diameter of 2 ft. often unbranched, but sometimes furnished with branches which grow out at right angles from the main stem, and then curve upwards and continue their growth parallel to it; these stems have from 12 to 20 ribs, on which, near the top at intervals of about an inch, are the buds with their thick, yellow cushions, from which issue five or six large and numerous smaller spines. The fruits, which are green oval bodies from 2 to 3 in. long, contain a crimson pulp from which the Indians prepare an excellent preserve; they also use the ripe fruit as food, gathering it with a forked stick attached to a long pole. Relatives of *Cereus* include some of our most interesting and beautiful hothouse plants. *Echinocereus pectinatus* produces a purplish fruit resembling a

gooseberry, which is very good eating; and the fleshy part of the stem itself is eaten as a vegetable after removing the spines. The climbing night-blooming cacti are included in the genera *Hylocereus*, *Selenicereus* and others, many bearing very large flowers.

EPIPHYLLUM and PHYLLOCACTUS (fig. 4), the leaf cactus, comprises 17 species, found in Mexico and Central and tropical South America. They differ from all the forms already noticed in being

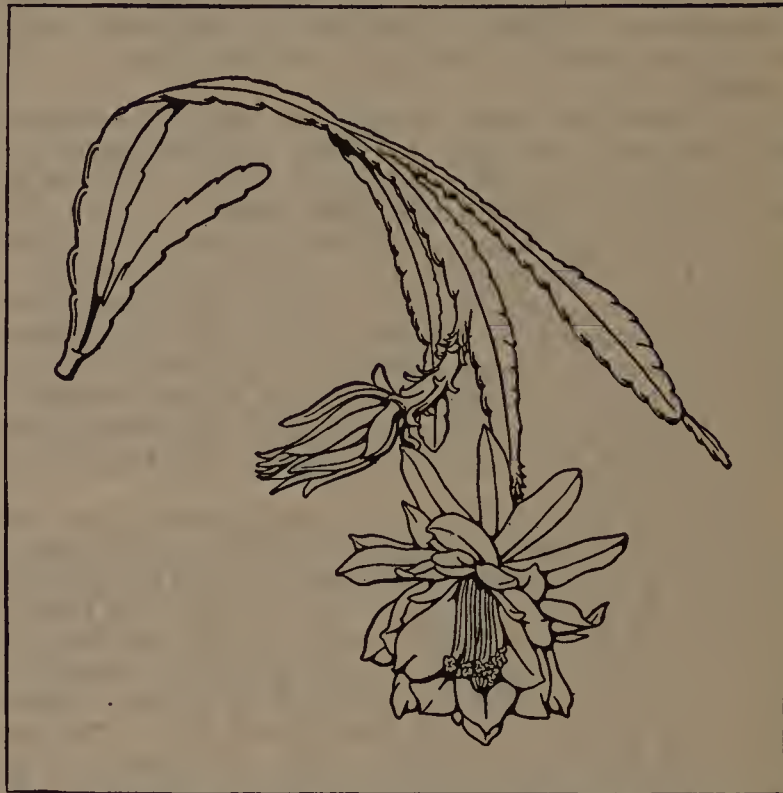


FIG. 4.—BRANCH OF THE LEAF CACTUS, AN ORNAMENTAL PLANT POPULAR IN GARDEN CULTURE. THE FLOWERS ARE 6 IN. OR MORE IN DIAMETER

epiphytial in habit, and in having the branches compressed and dilated so as to resemble thick fleshy leaves, with a strong median axis and woody base. The margins of these leaf-like branches are crenately notched, the notches representing buds, and from these crenatures the large showy flowers are produced. As garden plants these are amongst the most ornamental of the family, being of easy culture, free blooming and showy, the colour of the flowers ranging from rose-pink to creamy white. Relatives of *Epiphyllum* compose 8 other genera.

OPUNTIA, the prickly pear or Indian cactus, is a large group, comprising some 250 species, or more, found in North America, the West Indies and South America, extending as far as Chile. Some have been introduced into Australia with disastrous effects, since they have overrun large tracts of country. They are fleshy shrubs with rounded, woody stems and numerous succulent branches, composed in most of the species of separate joints or parts, which are often much compressed, elliptic or suborbicular, dotted over in spiral lines with small, fleshy, caducous leaves, in the axils of which are the areoles or tufts of barbed or hooked bristles, usually accompanied by spines. The flowers are mostly yellow or reddish yellow, and are succeeded by pear-shaped or egg-shaped fruits, having a broad scar at the top, mostly furnished on their soft, fleshy rind with tufts of small bristles. The sweet, juicy fruits of several species are much eaten under the name of prickly pears, and these are cultivated for their fruit in Southern Europe, the Canaries and northern Africa.

The cochineal insect (*q.v.*) is nurtured on the allied *Nopalea coccinellifera* and sometimes also on species of *Opuntia*. Planta-

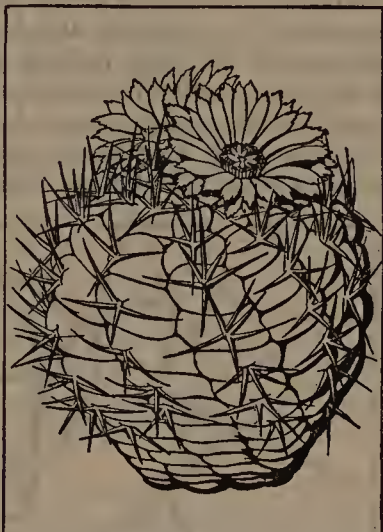


FIG. 3.—HEDGEHOG CACTUS (ECHINOCACTUS HEXAEDROPHORUS) COMMON IN THE DESERTS OF NORTH AND SOUTH AMERICA



FIG. 5.—ORGAN CACTUS IN THE DESERT SOUTH OF MEXICO CITY



tions, called nopaleries, are established for rearing this insect, *Coccus cacti*, and these often contain as many as 50,000 plants. Relatives of *Opuntia* form 6 other genera.

PERESKIA differs from the rest in having woody stems and leaf-bearing branches, the leaves being somewhat fleshy, but otherwise of the ordinary laminate character. One species, the Barbadoes gooseberry, climbs like the blackberry (*Rubus*) by recurved thorns; the others are spiny shrubs. The flowers are subpaniculate, white or yellowish. They are frequently used as a stock on which to graft other *Cacti*. There are about 19 species, mainly Mexican; *P. cubensis* is a peculiar little tree of eastern Cuba.

**ARBORETUM**, a place where trees and shrubs are cultivated for scientific, ornamental or other educational purposes; that portion of a botanical garden used for woody plants. There are many such collections of hardy plants in cities and private parks. Rich men often spare neither pains nor money to get important collections to adorn their estates, many of which have later been given to cities to be used as public parks. When properly maintained they make creditable arboreta. The modern arboreta contain plants as specimens or collections arranged according to some definite method—it may be systematic relationships, or commercial uses, or perhaps, to show ecological adaptations. The entire field of possibilities is seldom covered by any one arboretum, but each one specializes in a few projects for which it is particularly equipped or well situated.

As early as the middle of the 16th century René du Bellay of Touvoys, France, in co-operation with Pierre Belon made a good collection of trees and brought into France seeds of exotic species from western Asia. This collection long remained the richest and most beautiful in France or perhaps the world. About 1720, Duhamel du Monceau, head of the French Marine, and a scientist, gathered plants from all over Europe and North America to plant on his two estates. The plants were classified, arranged and planted in a methodical manner resulting in what might be called the first arboretum made with scientific purposes. From his experience with the collection, du Monceau wrote and published in 1755 a book on characteristics and cultivation of trees and shrubs. This collection of plants and the publication had a great influence on study and early distribution of imported plant species. Many of these imported types can still be found in France.

One of the most complete arboreta in the world is that at Kew, England, in the Royal Botanical Gardens. It had its beginnings as far back as 1762 though it was not thrown open to the public until 1841. To the latter date the ground, not exceeding 11 ac., had been held as a private estate by members of the royal family. In 1845 the pleasure grounds and Royal Gardens at Kew, occupied by the king of Hanover, were given to the nation and placed under the care of Sir William Hooker for the purpose of establishing an arboretum. Hooker and his son, Sir Joseph, kept steadily at the task until the gardens and arboretum were among the finest and most complete in the world. The arboretum monopolizes a large portion of the entire garden (288 ac.) with trees and shrubs representing some 4,500 species and varieties. In addition to the arboretum at Kew, important collections of trees and shrubs in Great Britain are those at the Royal Botanic Gardens in Edinburgh and at the Glasnevin Garden in Dublin, and a small select collection at Oxford. On the continent of Europe the classical example is the *Jardin des Plantes* in Paris. Here the gardens are very formal and make a striking effect.

In the United States the Arnold arboretum at Boston ranks with Kew in size and completeness. This institution had its beginnings in 1869 when James Arnold left in trust \$100,000 to be used for the promotion of agriculture or horticulture. Through an agreement made with Harvard college officials in 1872, the Arnold bequest was used together with a 125 ac. tract of land, bequeathed by Benjamin Bussey, for the establishment of a tree garden. Charles Sprague Sargent was made the first director. He held the position until his death in 1927. During this time he made a notable arboretum, the best in the United States and ranking favourably with the best in the world. Sargent left \$10,000 to the Arnold arboretum to be used with accumulated interest

200 years hence, at which time it will amount to millions of dollars. Its 260 ac. are planted with 6,536 species and varieties of trees, shrubs and vines belonging to 339 genera. Of these, 2,418 species or varieties are exotic, coming particularly from Japan, China, Siberia and the Himalayas. The Arnold arboretum by legal agreement is a part of the regular park system of the city of Boston, but, being under the management of a great university like Harvard, it has an aspect differing entirely from that of an ordinary park.

Among the other most outstanding arboreta in the United States are the Missouri Botanical garden in St. Louis, Mo., the Morton arboretum near Chicago, Ill., and the Hilland gardens in Rochester, New York. Three million dollars have been appropriated for the establishment of the Boyce Thompson arboretum in connection with the Boyce Thompson Institute for Plant Research, Yonkers, New York. The Boyce Thompson arboretum combines a large collection of trees and shrubs with a great plant research institute thus utilizing the greatest range of possibilities of an arboretum. The National arboretum at Washington, D. C., has received an appropriation of \$300,000 from the Government for the purchase of lands. Further appropriations will be given for buildings and maintenance as the needs arise. It will be a laboratory for the plant scientists of the U.S. Department of Agriculture. The California Botanical garden at Los Angeles, Calif., has received a gift of 2,000 ac. of land, part of which will be used for the arboretum and part of which can be sold for capital and maintenance.

The tendency of recent times is to manage arboreta so as to make them serviceable to the people. To serve most people an arboretum must have a scientific, an economic and a cultural aspect. On the scientific side the arboretum furnishes all types of hardy plants for the systematic botanist, the plant pathologist, the plant physiologist, the plant-breeder and the entomologist. From this will come a thorough study of diseases and rational control measures; a better knowledge of soil requirements and cultural methods; many new plant hybrids from controlled cross-breeding; and new methods of combating insect pests. The nurserymen and horticulturists look upon an arboretum as a place where plants are tested and displayed for the purpose of showing their economic possibilities. In this way the forester selects the species which fulfil specific needs for paper pulp, trees for hardwood lumber, etc. The nurserymen select from the arboretum species that they can fit into the landscape for the increasing demands of the public. Lastly, the public in general looks upon an arboretum as an unusually fine park, a place to go when in need of peaceful rest and a place that offers a chance to increase one's knowledge about nature. (See also BOTANIC GARDEN, FORESTRY and HORTICULTURE.) (P. W. Z.)

**INFLORESCENCE**, the arrangement of the flowers on the axis, or the ramification of the floral axis, composed of the *rachis*, which forms the stalk supporting the flower or cluster of flowers, called the *peduncle*. A flower having no stalk is called *sessile*. The floral axis may be shortened, assuming a flattened convex or concave form and bearing numerous flowers as in the artichoke, daisy, etc. There are two distinct types of inflorescence (1) *indeterminate*, *indefinite* or *axillary* and (2) *determinate*, *definite* or *terminal*. A third series of inflorescence is termed *mixed*. In the *compound indefinite* inflorescence the lateral shoots develop centripetally upon a primary axis into a group of racemes or compound racemes. See FLOWER.

**INVOLUCRE**. The whorl of bracts at the base of the inflorescences or general umbel in umbelliferous plants is called a *general involucre*; the similar leafy whorl adjoining the smaller umbels or umbellules being termed an *involcel* or *partial involucre*. In Compositae the name is applied to the bracts surrounding the head of the flower characteristics of this family and Umbelliferae. See FLOWER, UMBELLIFERAE and COMPOSITAE.

**GALLS**. This term may be applied to any excrescences caused in plants or animals by the action of living animals, usually insects. In animals, galls may be produced under the skin of mammals or birds by acarids or by dipterous insects. The term, however, is mostly confined to vegetable excrescences of a particular type.



Accepting the definition of Lacaze-Authiers they comprise "all abnormal vegetable productions developed on plants by the action of animals, more particularly by insects, whatever may be their form, bulk or situation."

**History.**—The hypertrophies of plant tissues known as galls have been known from early times. Theophrastus (372–286 B.C.) referred to the gall-nuts as an article of trade and to the superior quality of those from Syria. The nature of galls was, however unknown until recent times. It was naturally assumed that they arose spontaneously, *i.e.*, directly from the plant, without the intervention of any other animal or plant. John Evelyn, the diarist states in his *Sylva* (published 1664): "Pliny affirms that the Galls break out all together in one Night, about the beginning of June, and arrive to their full growth in one Day." Evelyn was familiar with the oak galls of commerce imported for their tannin content but he did not realize that the oaks in England bore numerous galls of different kinds—80–100 kinds are known. The association of insects with most galls appears to have been discovered by Martin Lister (1630–1712) who was physician to Queen Anne. Malpighi (1620–1694) the physician and botanist seems to have been the first to deal systematically with galls, publishing a treatise entitled *De Gallis* which dealt with the galls of Italy and Sicily. In England, Dr. Derham, Canon of Windsor, seems to have been the first to take up the study of galls; he refers to Malpighi's work in his Boyle Lectures given in 1711 and 1712.

**Nature.**—Galls arise from the abnormal development of meristematic tissue of the plant as a result of an abnormal stimulus. The stimulus is caused by an animal parasite. The parasite is usually an insect which lays an egg in the plant tissue but some galls are due to the action of eelworms (nematodes). The stimulus causing the abnormal development of the plant cells may be due in some cases to a chemical substance injected by the insect but in many cases, as in those of the wasps producing oak galls, gall formation is due to the action of the larva developing from the eggs; in this the movements of the larva probably play a part. It must be borne in mind that the gall is the result of the interaction of two living organisms, the plant and the parasite. It is true that the gall is built up out of the tissues of the plant, but its special form and structure depends on the nature of the animal. The interaction is made clear from the fact that the same plant attacked by different insects will produce very different galls. In fact the differences between galls on the same plant may be the best means of distinguishing the insects, as in the case of gall-gnats of the willow, where ten different species attack *Salix humilis*, the insects being almost impossible to distinguish in the fully grown state except by the galls they produce.

**Form.**—Galls are very variable in form and size but very constant for the special insect and special host plant concerned. Often the galls are entirely different from the structure on which they have developed or which they have replaced. Commonly, however, the tissues outside the larval chamber enclosing the insect, *i.e.*, tissues which give the gall its distinctive form, indicate the special organ (leaf, etc.) from which the gall has developed. In

the gall known as "Robin's pincushion" or "bedeguar" (produced by the action of the female gall-wasp, *Rhodites rosae*, on a leaf or bud in spring) the moss-like covering represents rudimentary leaves, consisting of fibro-vascular bundles with very little parenchyma between. Other galls represent in the case of the oak the arrested acorn. The size of the galls produced by insects varies enormously, some may be only a millimetre ( $\frac{1}{24}$  inch) or two in length while those on the roots of old oak trees may reach the size of a man's fist. Many of the various galls are brightly coloured.

**Classification.**—The most satisfactory classification is that by the insects which cause them and the plant on which they are produced. Different types can however be distinguished by their external appearance and internal structure. Most of them are unilocular or monothalamous (containing but one chamber or cell), while others are plurilocular (polythalamous), *i.e.*, many-celled and contain a number of insects. The ordinary oak galls produced by the attack of a wasp (*Cynips*) on a leaf bud of oak are unilocular. Following mainly Kerner and Oliver and Swanton (see Bibliography) galls may be distinguished as the *simple* and *compound*. The simple galls are produced from a single plant organ such as a leaf. These may again be distinguished as (1) *felt galls* where the epidermal cells become hypertrophied and grow into hair-like projections, and (2) *mantle galls* where a chamber is developed round the insect. Mantle galls may further be distinguished as *scroll galls* (where the leaf or petiole becomes rolled and thickened), *pocket galls* (where a pocket or excavated chamber is produced) and *covering galls* (where the insect is covered in by the over-arching of tissues but the tissues do not fuse where they meet, and finally shrivel and leave a slit for the escape of the insect). The simple galls also include (3) the *solid* or *tubercular galls* of which the well known spherical marble gall on the oak is a good example, and the root galls. In addition there are *compound galls* in the growth of which several organs of the plant are concerned. These may be (1) *bud-like galls* which may arise from modified foliage buds or modified flower buds; (2) *galls at the base of shoots*, where the upper part of the shoot continues a normal growth beyond the gall; (3) *rosette galls* which may be developed either in the foliage or the floral region.

**Causal Agents.**—As already stated insects are the chief agents while eelworms play a part, fungi not being properly included. Of the insects the classes concerned may be Hymenoptera (wasps and sawflies), Coleoptera (beetles), Lepidoptera (moths), Diptera (flies), as well as Hemiptera (aphides), and Acari (mites). The eelworms (Nematoda) belong to such genera as *Heterodera* and *Tylenchus*. Among the Hymenoptera (*q.v.*), the group *Cynipidae* (gall-wasps) are best known as gall producers. The members of this group (*e.g.*, *Cynips*, *Andricus*, *Biorrhiza*, *Rhodites*), have received more attention as gall producers than any other insects. This is partly due to the fact that they are responsible for many of the galls so commonly found on the oak but also to the fact that many of the insects show alternation of generation, *i.e.*, the young produced do not resemble their parents but their grandparents, and with these two different generations different galls may be associated. In the case, for example, of *Biorrhiza pallida* the female gall-wasp pricks the oak bud and lays its eggs therein with the result that the familiar gall known as "oak-apple" is produced. From this gall the wasps emerge in July, the males winged and the females wingless or with rudimentary wings only. The female, who is smaller than her parents, crawls down the oak trunk, reaches the ground, and then pierces the roots of the oak producing the other type of gall, the root gall. In other cases the same organ (leaf or bud) may be attacked in each case but different galls are produced. The gall-wasps are small insects with straight antennae and a compressed and usually very short abdomen with the second or second and third segments greatly developed, the rest concealing the partially coiled ovipositor. The transformation from the egg through the larval state to the imago (the perfect insect) takes place in the gall, the imago boring its way out of the gall usually in the autumn. Among the galls produced by *Cynips* and its allies are the "oak-apple" or "oak sponge" produced by *Andricus terminalis*, the currant or berry galls of



FROM: (A TO D) SWANTON, "BRITISH PLANT GALLS" (METHUEN & CO., LTD.); (E) CONNOLD, "PLANT GALLS OF GREAT BRITAIN" (ADLARD & SON, LTD.)

**VARIOUS PLANT GALLS CAUSED BY THE ATTACK OF INSECTS**

A. Gall on speedwell caused by fly *Perrisia*. B. Turgent of willow with leaves galled by fly (another species of *Perrisia*). C. Leaf of black poplar galled by aphid (*Pemphiquius*). D. Leaf of oak galled by gall wasp (*Dryophanta*). E. Various types of oak galls caused by gall wasp (*Cynips*)



*Spathegaster baccarum* and the "oak spangles" of *Neurotenes lenticularis*. The marble galls or "Devonshire woody galls" of oak buds which often destroy the leading shoots of young oak trees are produced by *Cynips Kollari*. They were first introduced into Devonshire about 1847 and after a time spread widely. The large purplish Mecca or Bassorah galls produced by *Cynips insana* have been regarded by some as the Dead Sea fruit, mad apple or apples of Sodom alluded to by Josephus and others, but more probably the fruit referred to is that of a species of *Asclepias*.

Oak galls or gall nuts (produced by cynips) were once a valuable article of commerce (for ink making, etc.)—they may contain as much as 70% of tannin. The "blue," "black" or "green" galls still contain the insect; the inferior "white" galls are lighter coloured and are gathered after the insect has escaped.

The saw-flies (also members of the Hymenoptera) so named on account of the saw-like nature of the egg depositing apparatus (the ovipositor) produce galls on willow, rose and other plants; on the willow, bud galls, stem galls and leaf galls are all produced. The red, oval or kidney shaped swellings on the blade of the willow leaf are perhaps the best known saw-fly galls in Great Britain. Of beetles (Coleoptera) in spite of their large numbers (150,000 or more species) only a very few are responsible for plant galls. Gorse and vetches may be attacked, and also the toadflax (*Linaria vulgaris*). *Ceuthorhynchus sulcicollis* attacks the underground portions of various plants (turnips, swedes, cabbages, etc.) of the family Cruciferae. The swellings produced are sometimes confused with the malformations due to the disease, "finger and toe," caused by a fungus *Plasmodiophora brassicae*.

Galls caused by moths (Lepidoptera) are also infrequent and not of great economic importance. *Rhyacionia resinella* produces a gall upon *Pinus silvestris*, destroying the terminal bud and thus retarding the growth of the tree. Among the flies (Diptera) those which cause galls belong mostly to the gallmidges (Cecidiomyidae). *Spiraea ulmaria* (meadowsweet) and *S. filipendula* are attacked by *Perrisia ulmariae*, the galls appearing as small, glabrous, light green pustules; over 200 have been counted on one leaf. The germander speedwell (*Veronica Chamaedrys*) and the nettle (*Urtica*) are "galled" by species of *Perrisia*, as are also willows. On willows a number of galls are also produced by species of *Rhabdophaga*. The frit-fly (*Oscinis frit*) causes the new shoots of cereals and pasture grasses to become swollen and distorted. The ash, maple, hornbeam, oak, grape-vine, alder, gooseberry, blackberry, pine, juniper, thistle and fennel are also galled by insects of this class. Among the order of Hemiptera, the Aphidae (green fly), the Psyllidae (plant lice) and the Coccidae (scale insects and mealy bugs) all include forms which are gall producers. The majority of these belong to the first class Aphidae the members of which are generally known as "blight" or "green-fly." Of the galls produced by aphids the best known are probably those found on the spruce fir (*Abies excelsa*), resembling immature cones in size and shape. They are sometimes called "pineapple" galls and are due to species of *Chermes*. The galls develop near one end of a twig and are large and plurilocular containing in some cases as many as twenty-five cavities; a single gall may contain 2,000 insects. The mites belonging to the order Acari of the class Arachnida (which includes the spiders and scorpions) are responsible for a number of galls. The gall-formers have only two pairs of legs, no eyes and belong to the group Vermiformia; they are very minute and are easily developed. The mite-galls are nearly always characterized by a felt of hairs which develop in association with the gall by the abnormal growth of the epidermal cells of the leaf attacked. These galls are mostly caused by species of the genus *Eriophyes*; they are found on the sycamore, pear, plum, ash, alder, vine, mulberry, etc. Those on the sycamore leaf due to *Eriophyes macrorrhynchus* are very common in Great Britain in June and July, and several hundred may be found on a single leaf. They are small, elongated outgrowths, about 2 mm. broad by 3 mm. long, tapering somewhat at the free end. They are bright red in colour with a tuft of hairs at the base and also bearing hairs in the hollow cavity and at the aperture of the gall; they are borne on the upper surface of the leaf. The gall-mite,

*Eriophyes ribis* causes "big-bud" in black currants and is a serious pest, while *Eriophyes pyri* is the pear leaf blister mite.

Among the order Nematoda the genera *Heterodera*, *Tylenchus* and *Aphelenchus* (belonging to the family Anguillulidae, to the members of which the term eelworms is applied) cause galls. Either the aerial or underground parts may be attacked. A number of the infections are of economic importance.

**Guest Flies.**—The insect galls often contain, besides the larva of the insect responsible for the gall, so called *inquilines* or lodgers. They feed on the substance of the gall and so deprive the normal "householder" of part of the food supplies and frequently kill off the rightful owner. There are also definite parasites (generally small Hymenoptera belonging to the family Chalcididae) which kill and devour not only the primary occupant of the gall but also the "guest flies." Derham, who has been already referred to, recognized in the early years of the 18th century that galls may contain interlopers. His quaint language may be quoted: "I apprehend we see many vermicules towards the outsides of many oak-apples, which I guess were not what the primitive insects laid up in the germ from which the oak-apple had its rise, but from some supervenient additional insects laid in after the apple was grown, and whilst it was tender and soft." The presence of different classes of insects within the same gall renders investigation very difficult.

**Fungi.**—A number of fungi cause marked malformations of the portions of the host plant attacked. For example, *Synchytrium endobioticum* causes wart-like outgrowths of the potato, *Plasmodiophora brassicae* swellings on turnip and cabbage roots. In these cases, however, the tissue of the outgrowth is usually penetrated by the fungus so they are hardly comparable to the insects galls, where the abnormal tissue is purely vegetable in nature and grows round the insect responsible for the malformation. A few cases which are sometimes confused with true galls may be mentioned. Cultivated plums, the sloe and the wild cherry may show a condition in which the fruit is swollen and deformed; this is known as "bladder plum" and is due to the attack of a fungus, *Exoascus pruni*, belonging to the class Ascomycetes (see FUNGI). The so-called witches' brooms (*q.v.*), are found on various trees and are sometimes mistaken for galls; they are conspicuous as groups of short, generally unhealthy twigs with reduced leaves, the branches of the "broom" growing upward. On birch these brooms may be caused by the fungus *Exoascus turgidus* though they may also be caused by a mite of the genus *Eriophyes*. Those on cherry are due to *Exoascus cerasi*, and those on silver fir are due to the attack of a rust fungus *Melanosporella elatina*. The large succulent often reddish swellings found on the leaves of the cowberry (*Vaccinium Vitis-idaea*) and the cranberry (*Oxycoccus quadripetalus*) and the still larger ones on species of *Rhododendron* are due to fungi belonging to the genus *Exobasidium* (see FUNGI).

For further details see A. Kerner von Marilaur, *Natural History of Plants*, Vol. II. (trans., F. W. Oliver, London, 1894); N. Adler and C. Straton, *Alternating Generations: A Biological Study of Oak Galls and Gall Flies* (London, 1894); E. T. Connold, *British Vegetable Galls* (London, 1901); *British Oak Galls* (London, 1908); *Plant Galls of Great Britain* (London, 1909); E. Küster, *Die Gallen des Pflanzen* (Leipzig, 1911); E. W. Swanton, *British Plant Galls* (London, 1912). (V. H. B.)

**HEREDITY (in plants). Flower Colour.**—Flower colour has been more extensively studied than any other character. Thus in *Primula sinensis*, in which more genes are known than in any other flower (28 in all), 11 affect flower colour, while 3 others determine the size of the "eye" or central coloured patch, the remainder affecting structural characters, such as leaf shape and habit of the plant. Many of the genes affect several parts. Thus the same gene causes crimping of the leaves and petals, and the light-coloured flowers due to several recessive genes are associated with light stems and leaves.

Flower colour may be due to red or blue anthocyanin in the sap, to yellow pigment in the plastids, or to both. The combination is generally purple or orange. Some plants, *e.g.*, the primrose, have no anthocyanin, others, such as *Primula sinensis*, no yellow pigment, while many, *e.g.*, the rose, tulip and stock,



have both. Usually each pigment is governed by a separate set of genes. Loss of the principal gene or genes determining anthocyanin formation gives a yellow plant if plastid pigments are present, otherwise a white. Similarly loss of the principal gene for yellow may convert a bronze into a red. In addition either the anthocyanin or the plastids may be whitened by a dominant gene. A gene may alter the colour of the anthocyanin either by altering the reaction of the cell-sap (for blue anthocyanin is generally reddened by acid) or by altering its molecular structure. The genes which cause large changes in flower colour (*e.g.*, turn a white into a coloured plant) often affect leaf and stem colour too. They may also affect structural characters. Thus whiteness in stocks may be due to the loss of either of two genes. A white stock cannot have hairy leaves. The hairiness or otherwise of the coloured plants is determined by two further dominant genes.

**Cereals.**—Maize has been very thoroughly analysed, and the inheritance of many economically important characters is understood. Thus the sugary endosperm of the sweet corn is due to a recessive gene, and another recessive gene determines waxy endosperm. But most cultivated wheats and oats are hexaploids, though a few are tetraploids. They are moreover allohexaploids. Hence while certain characters behave in a Mendelian manner, the same character may be due to a gene in either of the three sets of chromosomes, and will therefore exhibit different linkages in different races. Moreover, as usual in allopolyploids, characters which behave as recessives in  $F_1$  do not always reappear in  $F_2$ . The characters known to be Mendelian are not in general those of the greatest economic importance. Resistance to disease varies in its inheritance with the species of rust or mildew concerned. Thus resistance to yellow rust, *Puccinia glumarum*, is recessive, but that to brown rust, *Puccinia triticina*, and mildew, *Erysiphe graminis*, are dominant. But the matter is greatly complicated by the fact that a wheat which is immune in one environment may be attacked in another, owing to the existence of different races of the same parasite species.

**Anisogeny.**—Among the structural and physiological characters which have been found to obey Mendel's laws are size, habit, leaf shape, flower shape, time of flowering, heterostylism, sterility of either male or female organs, hairiness, and a variety of abnormalities. An occasional complication of plant genetics is anisogeny, *i.e.*, the ovules and pollen grains are of different genetical composition. This may be due to differences in the cytoplasm or plastids which are maternally inherited, to only half the pollen grains being functional or, in dioecious plants to sex-linkage. Thus in the stock, *Matthiola incana*, a race exists which, though single, gives slightly more than 50% of double flowered plants when self-fertilized. When used as a female with a normal single, half the  $F_1$  produce doubles; when used as a male all the  $F_1$  do so. But doubleness now behaves as an ordinary recessive. This is generally explained on the view that the dominant gene  $S$  for singleness is closely linked with a gene  $p$  which prevents the proper functioning of pollen grains bearing it. The ever-sporting type is  $\frac{sp}{SP}$ . All its functional pollen is  $sP$ , so that

when selfed, about half the seeds are  $\frac{SP}{sp}$  and give doubles, the other half perpetuating the parental type. The gene inhibiting plastid colour is carried in the same chromosome.

**Unicellular Organisms.**—In Protista, including Bacteria and certain algae, any cell can reproduce, and there is no clear distinction between growth and reproduction. Where reproduction is asexual we have a condition parallel to that of a clone in the higher plants, and variations are rather feebly inherited. Nevertheless selection has sometimes been at least temporarily effective within such a clone. When sexual reproduction occurs, there is often a marked outbreak of variation. Acquired characters, such as those produced by certain poisons in trypanosomes, are inherited at least for a considerable period but are generally lost on sexual reproduction, and sometimes without it. Adaptive characters acquired by a strain of micro-organisms, *e.g.*, a capacity for fermenting sugars not usually attacked, may be genuine adaptations inherited, but are sometimes believed to be

due to the selection of mutants.

**Species Crosses.**—When two species with different chromosome numbers are successfully crossed the reduction divisions of the hybrid are generally irregular, and it is nearly or quite sterile. Occasionally in such cases unreduced gametes may be formed, in which case there is no segregation of characters, and allopolyploidy may result in later generations. When however the chromosome numbers are equal, the normal segregation mechanism may be able to function, though it does not always do so. In this case the  $F_2$  generation, and the results of back-crossing  $F_1$  to either parent, are usually polymorphic, and may include monstrous or more or less inviable forms. In certain cases, owing to the inviability of most gametic and zygotic combinations, the  $F_2$  consists entirely of types resembling one or other parent fairly closely. Sometimes however a partial Mendelian analysis is possible. For example from the cross between the primrose, *Primula acaulis*, and the blue Asiatic primrose, *Primula juliae*, it appears that the former possesses a gene for yellow pigment, the latter for anthocyanin, so that whites appear in  $F_2$ . If the oxlip, *P. elatior*, is crossed with *Juliae* it is found to carry a gene inhibiting anthocyanin formation and one for the umbellate habit as well as those of *acaulis*. At least two genes are concerned in determining hairiness in these crosses, one being linked with a colour gene. Besides genes, species may differ in cytoplasmic factors, as do *Geranium striatum* and *G. Endressii*, and the commonness of variegation as the result of species crosses suggests that the plastids may also differ. Mendelian analysis has been carried some way in specific crosses of the moths of the sub-family Bistoninae, and some other animals, but it is complicated not only by sterility and upsets of sex (*q.v.*), but by the effects of heterosis, which cause increase in size and vigour.

Where species cannot be crossed their genetics and chromosomal architecture can be compared; thus the Norway rat, *Rattus norvegicus*, has three linked autosomal genes,  $C$ ,  $R$  and  $P$  whose loss causes albinism, red-eyed yellowness and pink-eyed yellowness respectively.  $C$  and  $P$  have also been lost in different mouse races, and are linked with somewhat greater intensity,  $R$  has been lost in the black rat *Rattus rattus*,  $C$  and  $R$  in the Californian deer-mouse, *Peromyscus maniculatus*, where they are also linked. Clearly the architecture of the germ-plasm is similar in these species. On the other hand the arrangement of the genes in the chromosomes differs appreciably in different species of *Drosophila*, and sectors of a chromosome have been reversed in certain geographical races of *D. melanogaster*. In the rodents certain species and varieties differ by colour genes which are multiple allelomorphs of those producing well marked changes such as yellowness; that is to say that these particular genes differ less between species than domestic varieties. . . . (J. B. S. H.)

**INSECTIVOROUS PLANTS.** Insectivorous or, as they are sometimes more correctly termed, carnivorous plants are, like the parasites, the climbers or the succulents, a physiological assemblage belonging to a number of distinct natural orders. They agree in the extraordinary habit of adding to the supplies of nitrogenous material, afforded them in common with other plants by the soil and atmosphere, by the capture and consumption of insects and other small animals. The curious and varied mechanical arrangements by which these supplies of animal food are utilized are described under the headings of the plants.

The best known and most important family of insectivorous plants—Droseraceae—includes six genera: *Byblis*, *Roridula*, *Drosera*, *Drosophyllum*, *Aldrovanda* and *Dionaea*, of which the last three are monotypic, *i.e.*, include only one species. The Sarracenaceae contain the genera *Sarracenia*, *Darlingtonia*, *Heliamphora*, while the true pitcher plants or Nepenthaceae consist of the single large genus *Nepenthes*. These three families are closely allied and form the series Sarraceniales of the free-petalled section (Choripetalae) of Dicotyledons. The curious pitcher-plant, *Cephalotus follicularis*, comprises a separate family, Cephalotaceae, closely allied to the Saxifragaceae. Finally the genera *Pinguicula*, *Utricularia*, *Genlisea* and *Polypompholix* belong to the gamopetalous family Lentibulariaceae.

While the large genus *Drosera* has an all but world-wide dis-





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### INSECTIVOROUS PLANTS

Certain plants, as sundews, butterworts, bladderworts and pitcher-plants, supplement their food supply by capturing and consuming insects and other small animals, being provided with special struc-

tures for entrapping and digesting their prey. Venus's fly-trap, for example, has hinged leaves which suddenly close upon insects that alight thereon. For details see articles on the plants illustrated

1. Trumpets (*Sarracenia flava*); 1A. Pitcher-like leaves. 2. California Pitcher-plant (*Darlingtonia californica*); 2A. Young pitchers. 3. Northern Pitcher-plant (*Sarracenia purpurea*);

3A. Pitcher-like leaves. 4. Parrot-headed Pitcher-plant (*Sarracenia psittacina*); 4A. Pitcher-like leaves. 5. Red Trumpet-leaf (*Sarracenia rubra*); 5A. Leaves of the plant. 6. Venus's Fly-trap (*Dionaea muscipula*); 6A. Fly-catching leaves.

7. Sundew (*Drosera intermedia*). 8. Mindoroan Pitcher-plant (*Nepenthes Burkei*), Philippine Is.; 8A. Leaf pitchers. 9. Yellow Butterwort (*Pinguicula lutea*); 9A. Viscid leaves







tribution, its congeners are restricted to well-defined and usually comparatively small areas. Thus *Drosophyllum* occurs only in Portugal and Morocco, *Byblis* in tropical Australia, and, although *Aldrovanda* is found in Queensland, in Bengal and in Europe, a wide distribution explained by its aquatic habit, *Dionaea* is restricted to a few localities in North and South Carolina. *Cephalotus* occurs only near Albany in Western Australia, *Heliamphora* on the Roraima Mountains in Venezuela, *Darlingtonia* on the Sierra Nevada of California, and these three genera too are as yet monotypic; of *Sarracenia*, however, there are seven known species scattered over eastern North America but mostly in the south-eastern United States. The 60 species of *Nepenthes* are mostly natives of the hotter parts of the Indian Archipelago, but a few range into Ceylon, Bengal, Cochin China, and some even occur in tropical Australia on the one hand, and in the Seychelles and Madagascar on the other. *Pinguicula* is abundant in the north temperate zone, and ranges down the Andes as far as Patagonia; the 210 species of *Utricularia* are mostly aquatic, and some are found in all save polar regions. It is remarkable that all the insectivorous plants agree in inhabiting damp heaths, bogs, marshes and similar situations where water is abundant, but where they are not brought into contact with the plenteous supply of inorganic food as are the roots of most terrestrial plants.

**VEGETABLE**, a word used as a general term for plants (*q.v.*), and specifically, in popular language, for such plants as can be eaten by man or animals, whether cooked or raw, and whether the whole of such plants are edible, or only the leaves or the roots or tubers. Among such edible or culinary plants or portions of plants, a further distinction is made popularly between "fruits" and "vegetables," for which see **FRUIT**.

For the botany of vegetables see under the specific names, *e.g.*, **POTATO**, **TURNIP**, etc., and also **HORTICULTURE**, generally.

**ALGAE**. The algae comprise seaweeds, pond-scums, and a great variety of microscopic plants inhabiting fresh and salt waters in countless numbers. Many are found in or on the soil or on rocks and tree-trunks, and no region of the earth is devoid of them (see *Occurrence and Distribution*). The Latin *alga* means seaweed and only later acquired its present wider meaning. The algae belong to the lowest division (Thallophyta) of the vegetable kingdom, and are distinguished from the majority of higher plants by their simple reproductive organs and by the fact that their vegetative body as a general rule has a relatively simple construction; it is usual to speak of the body of the bigger algae as a *thallus*. All algae are holophytic; *i.e.*, they contain chlorophyll which enables them to use the energy of sunlight and to build up in the process of photosynthesis the organic compounds forming their body from carbon dioxide, water, and other simple substances. This distinguishes them from the fungi, the other subdivision of the Thallophyta. On the other hand it is very difficult to separate the algae from those groups of Flagellata which are holophytic (see *Phylogeny* and **PROTOPHYTA**). Most algae can only be studied with the help of a microscope, although no very high powers are necessary to make out the essential features.

### STRUCTURE AND REPRODUCTION

The algae exhibit a diversity of form not found in any other group of plants, ranging from one-celled organisms through manifold colonial types to simple or branched rows of cells (filaments) and onwards to elaborate massive growths attaining dimensions and complexities of structure that sometimes vie with those of flowering plants. The group is of great interest to the evolutionist, because it affords all possible stages in the evolution of a plant-body.

**Unicellular and Colonial Forms.**—Simplest are the unicellular individuals which are commonly spherical or oblong and usually enveloped by a firm cell-wall. The protoplasm of such cells resembles that of other plants in possessing a nucleus and one or more chromatophores containing chlorophyll and other pigments. Many unicellular algae (*e.g.*, *Chlamydomonas*, fig. 1, A) move freely with the help of delicate prolongations of the protoplasm, the cilia, which arise usually at the front end and

push the cell through the water by a movement somewhat like that of the arms of a human being whilst swimming. Motile individuals may be aggregated into colonies of diverse shape (*Pandorina*, fig. 1, B; *Volvox*, fig. 2, A), moving by the united action of all the cilia. The cells of these algae are often provided with a red streak or dot, the eye-spot, and two or more pulsating vacuoles near the front end, structures which they have in common with many unicellular animals.

Multiplication is effected by successive divisions of the protoplasm into 2, 4, 8, etc., parts, which secrete new membranes and gradually acquire all the parent's characteristics; in the colonial types each cell may divide in this way to produce a new colony. Reproduction is often preceded by withdrawal of the cilia and cessation of movement. In numerous unicellular and colonial algae this motionless state is the usual one. Naked motile cells (*zoospores*, see below) may be formed as a means of reproduction (*Chlorococcum*) or the power of movement is altogether suppressed and the new individuals are motionless from the first (*e.g.*, *Chlorella*, fig. 1, C and the colonial *Scenedesmus*, fig. 1, D). At times the progeny of a motile unicell (*e.g.*, *Chlamydomonas*) fail to acquire cilia and remain encased within the mucilaginous membrane of the parent; this may happen to successive generations and result in the formation of large jelly-like masses, from which the contained cells may ultimately escape as swimmers. In some algae (*Tetraspora*, *Gloeocapsa*, fig. 1, E) this palmelloid state is the normal one. There is little doubt that the motionless have in most cases evolved from motile types in one or other of the ways just indicated.

**Filamentous Forms.**—Many pond-scums and small seaweeds are filamentous, consisting sometimes of a simple row of similar cells (*Ulothrix*, fig. 1, F; *Tribonema*, fig. 2, P), although in most there is repeated branching; all the branches may be alike (*Ectocarpus*, fig. 1, H) or some may stand out as main axes bearing smaller lateral branches, which often arise in bunches (*e.g.*, *Batrachospermum*, fig. 4, A). Filamentous algae commonly reproduce by *zoospores*, *i.e.*, naked ciliated bodies formed (with or without previous division) from the protoplasm of ordinary (fig. 1, G) or specially enlarged (fig. 3, A) cells and liberated through a hole in the wall. The close similarity of these zoospores to the motile individuals of the same class warrants the assumption that the filamentous algae have evolved from such motile unicells, the method of their origin being illustrated by the way in which the zoospores proceed to produce new filaments. Their movements may continue for half an hour up to two or three days; but ultimately they settle down on some firm substratum, withdraw the cilia, and secrete a membrane. The end in touch with the substratum spreads out into a lobed holdfast (fig. 1, P), whilst the other rapidly lengthens and divides to form the thread, which in quiet water soon breaks away from its holdfast and floats freely. In rivers or in the sea the attachment is more permanent. In all filamentous forms, however, propagation by detached pieces of the threads (fragmentation) is frequent.

In many filamentous algae the thallus is composed of two branched systems, the one creeping upon some substratum and bearing the other which floats out into the water (*e.g.*, *Stigeoclonium*, fig. 2, D, and many of the simpler seaweeds). By suppression of the projecting system purely prostrate forms result, in some of which the branching is so dense that the threads fit together to form one-layered discs (fig. 2, E). All these and many other smaller algae are commonly found attached to larger ones or to aquatic flowering plants; *i.e.*, they are *epiphytes*.

Every cell of the simpler filamentous algae can enlarge and divide to form new cells, thus leading to a lengthening of the thread, but in the branched types such growth is often restricted to definite regions (*e.g.*, at the bases of the hair-like tips in many brown seaweeds, fig. 1, H) or confined to the end cell of each branch (*Cladophora*).

**Structure of Seaweeds.**—Such apical growth is usual in many filamentous seaweeds, most of which possess a more elaborate structure than the freshwater forms. The segments cut off from the apical cell often divide lengthwise as well as crosswise, so that the filament consists of several longitudinal series of cells which



commonly show a definite arrangement in tiers (e.g., *Sphacelaria*, fig. 1, I). In the older parts of many filamentous seaweeds a further complication of structure results from the outgrowth of cortical threads, either from the basal cells of the branches (*Batrachospermum*, fig. 4, A') or merely from the superficial cells of the thread itself; these apply themselves closely to its surface and form a dense small-celled investment which may become many layers thick and completely hide the original thread.

The thallus of some seaweeds is built up by the close juxtaposition of many filaments. In such there is a central cord or axis consisting of numerous longitudinal threads which are often more or less intertwined and which bear large numbers of short branches, projecting approximately at right angles and uniting to form a surface of varying degrees of compactness (fig. 1, J). Many of these forms appear to the naked eye as rather thick little branched threads (*Nemalion*, *Castagnea*), but seaweeds of quite a different outward shape may possess the same construction.

Many seaweeds are flattened and leafy, but such forms have doubtless originated from filamentous types in the course of evolution. Some in fact begin life as a simple filament and the derivation from a branched thread may even be decipherable in sections of the mature alga. In *Ulva* (sea lettuce) and *Porphyra* the thalli are thin flat sheets composed of uniform cells without localized growth, but in carrageen (fig. 4, F) and the brown *Dictyota* there are special apical cells at the tips of the numerous flattened branches and these have a firmer texture, being composed of three or more layers of cells, the inner ones usually much larger than the outer (see fig. 3, J).

The most complex structure is found in the large brown seaweeds (Laminariales and Fucales). Here it is usually possible to distinguish stalk and blade (e.g., *Laminaria*, fig. 1, K) and the latter may show a central thickened region (midrib) as in the Bladderwrack. In *Lessonia* (fig. 3, G) the stalk may have the thickness of a man's thigh and bears at its apex numerous long blades, the whole resembling a small tree. The bulky thalli, which are often several yards from base to apex, are attached by elaborate holdfasts, fingerlike in Laminariales, suckerlike in Fucales, and often clinging tenaciously to the rocks. In sections of the stalks it is easy to distinguish a central medulla of very irregularly arranged and prevalently elongate cells serving as a strengthening cord and for the conduction of food-substance, a wide cortex of broader cells storing food-reserves, and a superficial assimilatory region of small cells with many chromatophores. The surface cells at times divide abundantly and thus lead to the progressive increase in thickness of the stalk. The most striking of these large forms is *Sargassum* (fig. 1, L), where the cylindrical stalks bear numerous leafy outgrowths provided with a midrib and bearing in their axils small branch-systems, either terminating in air-bladders or containing reproductive organs.

Most algae possess a slimy feeling owing to the mucilaginous quality of the cell-walls. This feature is specially pronounced in the larger seaweeds and particularly in those inhabiting the stretch of shore between tidelevels, where the capacity of mucilage to absorb and retain moisture no doubt constitutes a protection against drying.

**Chromatophores.**—The chlorophyll and other pigments that give different algae their distinctive colours are (except Myxophyceae, see below) contained in special chromatophores, which are of diverse shape and size and in some groups are of great importance for the identification of genera and species. They are usually parietal (i.e., located in the protoplasm just beneath the cell-walls, fig. 1, C and F), but in some green and red forms they are axile (i.e., in the centre of the cell, fig. 2, G). In green algae the cells commonly contain only one or a few large chromatophores, but in the other classes they are usually more numerous and simpler in form, often appearing as little lens-shaped bodies (fig. 2, P). Embedded in the substance of the chromatophore are often found conspicuous rounded bodies, the *pyrenoids* (fig. 1, A and F), which consist of protein. Their exact purpose is not yet clear. In the green algae the pyrenoids are usually surrounded by starch, so that treatment with iodine renders them very conspicuous.

**Asexual Reproduction.**—The purely vegetative multiplica-

tion of algae by fragmentation of the threads has already been mentioned and fragments of the thallus may even, in the more elaborate forms under suitable conditions, give rise to a new organism. In most algae, however, a more specialized method (asexual reproduction), involving the liberation of spores formed from the entire or subdivided protoplasm of the cells, occurs at certain times. Many produce ciliated zoospores (cf. above) which are always without a wall and vary in character in the different classes; in more advanced types (e.g., *Ectocarpus*, fig. 3, A) they are produced within larger cells (sporangia), often differing in shape from the others and sometimes restricted to definite parts of the body. The zoospores may at times fail to develop cilia, secreting a thin wall already prior to their liberation. Such aplanospores are clearly zoospores which have lost the power of movement, and possibly illustrate the mode of origin of the motionless spores found in many algae lacking zoospores altogether. Thus, in most red seaweeds the sporangia produce four such motionless spores (tetraspores, fig. 4, C).

**Sexual Reproduction.**—A large number of algae exhibit sexual reproduction and all stages in its evolution may be found within the group. In the simplest cases (e.g., *Ulothrix*, *Ectocarpus*) the sexual cells or gametes, except for smaller dimensions, essentially resemble the zoospores and are formed in the same way. After a period of movement they meet in pairs and gradually fuse (fig. 1, Q) their nuclei fusing at the same time. Often the fusing gametes are identical in all respects (isogamy), although probably always derived from distinct individuals. In other cases there are two kinds of gametes (anisogamy) which may either merely differ in behaviour, one coming to rest before fusion occurs (e.g., *Ectocarpus*), or more commonly the passive gamete is larger and more liberally supplied with chromatophores than the other (e.g., *Cutleria*, fig. 1, O).

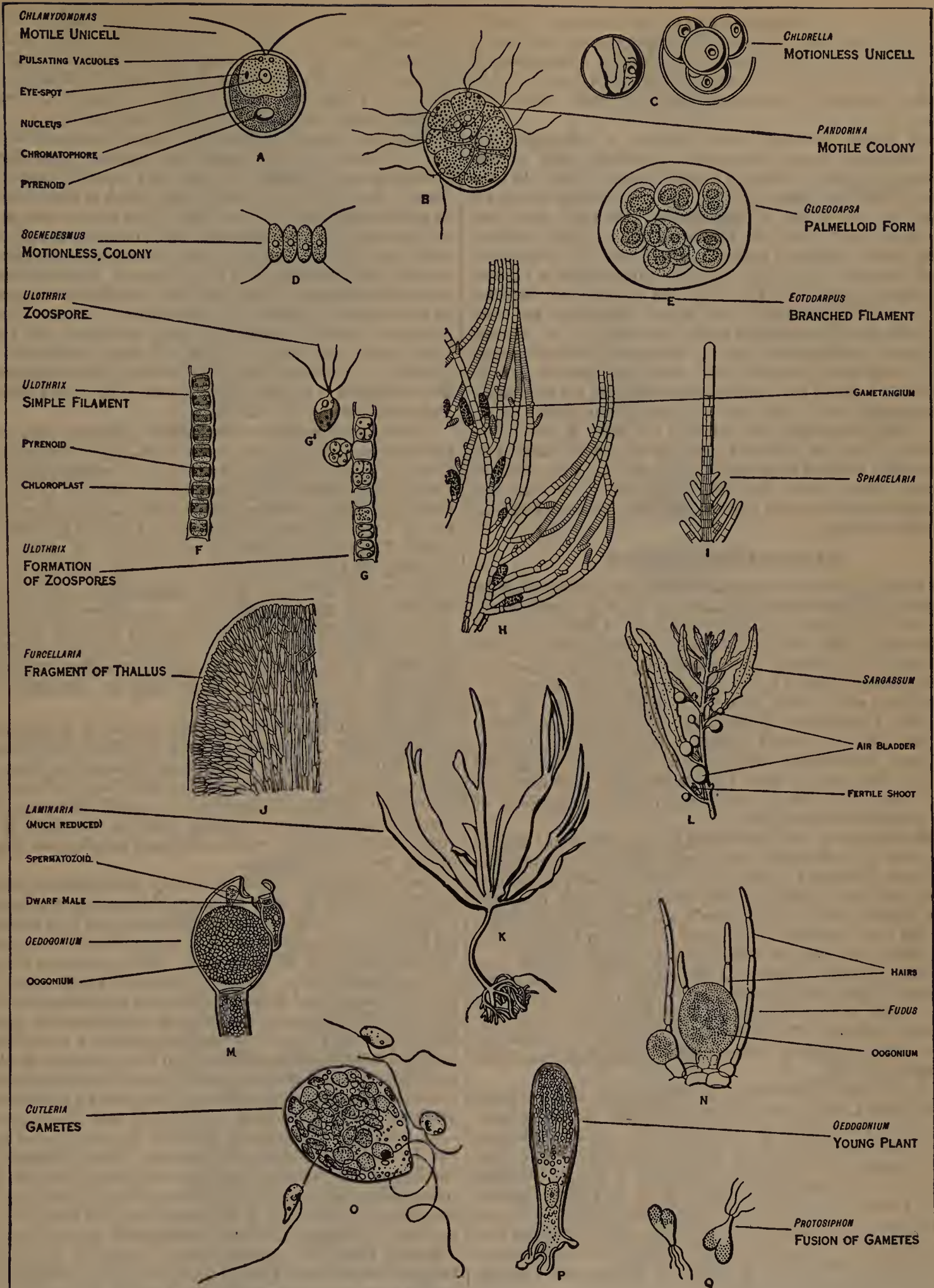
The advanced algae exhibit greater differences between the sexual cells (oogamy), the female or ovum being large, motionless, and provided with abundant chromatophores, the ciliated male or spermatozoid minute, actively motile, and consisting mainly of a nucleus with a thin covering of protoplasm (e.g., *Vaucheria*, *Fucus*). Ova and spermatozooids are formed within special cells (sexual organs) of diverse types; the oogonia (fig. 1, M and N; 2, J) harbouring one or, more rarely, several ova, are larger than the antheridia, which mostly produce many spermatozooids of a pale colour (often yellow). As a general rule the ovum remains inside the oogonium whose wall develops an aperture through which the spermatozoid swims and fuses with (i.e., fertilizes) the ovum. The red seaweeds have motionless male cells which are drifted by currents to the female organs (fig. 4, B). The unicellular sexual organs of most algae offer a sharp contrast to those of Bryophyta (liverworts and mosses).

The sexual cells are always devoid of a membrane, but after fusion the zygote soon secretes a thin wall and in seaweeds immediately proceeds to divide to form a new individual; in freshwater algae, however, the membrane is usually thick and a resting spore, often with yellow or red contents, results. Sexual cells may occasionally develop into new individuals without fusion, but in the oogamous types this is only rarely observed (*Cutleria*, *Chara*).

**The Life-cycle.**—The marked polymorphism, formerly ascribed especially to the simpler algae, is now disproved. A few occasionally assume forms differing considerably from the normal. Thus, various filamentous algae at times pass into a palmelloid condition, resembling that described for *Chlamydomonas*.

The alternation between sexual (gametophyte) and asexual (sporophyte) individuals, which is such a prominent feature of the life-cycle of the higher plants, is exhibited in varied ways among the algae. The green forms mostly show no clear alternation, the sexually formed spores, on germination, usually producing a few (often four) zoospores or aplanospores which form the new individuals. In *Coleochaete* there is more extensive division of the spore, a mass of 16 or 32 cells being formed, each of which can produce a new plant. This mass of cells is sometimes called a sporophyte, the ordinary *Coleochaete*-disc (fig. 2, E) bearing the sexual organs, being the gametophyte; but since reduction in chromosome-number (see CYTOLOGY) occurs at the first





A, B, E, AND Q FROM ENGLER AND PRANTL, "PFLANZENFAMILIEN," BY PERMISSION OF WILHELM ENGELMANN. C, F, G, H, J, L, M, O FROM OLTMANN'S, "MORPHOLOGIE U. BIOLOGIE D. ALGEN," BY PERMISSION OF GUSTAV FISCHER. D AND P FROM WEST AND FRITSCH, "BRITISH FRESHWATER ALGAE," BY PERMISSION OF CAMBRIDGE UNIVERSITY PRESS. K FROM FRITSCH AND SALISBURY, "AN INTRODUCTION TO THE STRUCTURE AND REPRODUCTION OF PLANTS," BY PERMISSION OF G. BELL AND SONS, LTD. N FROM HAUCK, "MEERESALGEN," BY PERMISSION OF EDUARD KUMMER. ALL EXCEPT K AND L CONSIDERABLY MAGNIFIED

FIG. 1.—STRUCTURE AND REPRODUCTION OF UNICELLULAR, COLONIAL AND FILAMENTOUS FORMS

Algae, the botanical group which includes seaweeds, pond-scum, and a great variety of microscopic plants, inhabit fresh and salt water, are found on or in the soil and on rocks and tree trunks in every region of the world. They comprise, with the fungi, the lowest division of

the vegetable kingdom (Thallophytes). Algae contain a green substance called chlorophyll which enables them in the presence of sunlight to build up their bodies from carbon dioxide, water and other simple substances. Fungi, having no chlorophyll, cannot do this



division in the fertilized ovum (as in all green algae), the sporophyte lacks the double chromosome-number usually regarded as characteristic of it. The simpler red seaweeds (Nemalionales) show the same features, the sporophyte here being represented by a bunch of threads that sprout out from the female organ after fertilization.

Among brown seaweeds many instances of alternation are known, where the asexual and sexual individuals differ in their chromosome-number in the same way as in higher plants. In some (*Pilayella*, *Dictyota*) the two generations are identical, except for this and for the kinds of reproductive structures they bear (homologous alternation). In *Laminaria* and its allies, however, they are sharply distinct (antithetic alternation), the sporophyte being an elaborate plant (fig. 1, K), the gametophyte a filament of microscopic dimensions (fig. 3, H). In *Cutleria*, on the other hand, the ribbon-like thalli of the sexual individuals are more conspicuous than the flat crusts of the asexual (fig. 3, F). Certain facts appear to indicate that, even in these cases, the two generations may originally have been alike. Most red seaweeds (except Nemalionales) show a true homologous alternation, the sporophyte with tetraspores (fig. 4, C) and the gametophyte bearing sexual organs closely resembling one another; but there is the curious complication that the fertilized ovum gives rise to bunches of threads which produce carpospores, and it is from these that the tetrasporic plants arise. In these forms there are thus two different sporophytes arising from one another, the second producing the gametophyte.

#### CLASSIFICATION OF ALGAE

The various classes of algae are essentially distinguished by the pigments in their chromatophores, the kinds of reserve-foods stored after photosynthesis, and the nature of their reproductive structures. They are:—I. Isokontae (Chlorophyceae), the green algae; II. Charales, the stoneworts; III. Heterokontae, the yellow-green algae; IV. Bacillariales (*q.v.*), the diatoms; V. Phaeophyceae, the brown algae; VI. Rhodophyceae, the red algae; VII. Myxophyceae (Cyanophyceae), the blue-green algae. There are, however, various groups of Flagellata (*e.g.*, Chrysomonadineae, Peridinieae) which include some algal forms and should no doubt rank as algae (*see* PROTOPHYTA), but the scope of this article is restricted to the above classes, the majority of whose members are true algae.

**Green Algae.**—I. The ISOKONTAE (CHLOROPHYCEAE) include a wide range of forms which are mainly freshwater or terrestrial, though most Siphonales are marine. They are readily recognized by their dark green colour and the storage of starch (coloured blue by iodine). The chromatophores are here chloroplasts containing the same pigments (chlorophyll, etc.) as in higher plants, though often possessing an elaborate shape and frequently provided with pyrenoids surrounded by starch. The motile stages (including zoospores and gametes) bear equal cilia (often two or four) attached to the front end. Cellulose frequently predominates in the cell-wall. The majority of Isokontae are isogamous and the gametes, except in the few oogamous types, are produced in the ordinary cells.

The motile forms are classed as VOLVOCALES, which include the unicellular *Chlamydomonas* (fig. 1, A) and various colonial types such as *Pandorina* (fig. 1, B), *Eudorina* (with 32 spherical cells arranged round the edge of a mucilage-sphere), and *Volvox* (fig. 2, A), where the colonies are composed of several thousand cells, all four often abundant in small pools. In *Volvox* the production of new colonies is restricted to special larger cells, and both this genus and *Eudorina* are oogamous. The Volvocales also include palmelloid forms, such as *Tetraspora* whose delicate green mucilage-masses, with the cells in groups of four, are common attached to water-plants in spring.

The motionless CHLOROCOCCALES (=Protococcales) comprise *Chlorococcum* (on damp soil), *Chlorochytrium* with large cells inhabiting the air spaces of the duckweed, and *Trebouxia* (=Cystococcus) which is found in many lichens and possesses an axile chloroplast. These three unicellular forms reproduce by zoospores, but the latter are lacking in *Chlorella* (fig. 1, C), which

is common in contaminated waters (*e.g.*, sewage) and also occurs as "green cells" in various animals (*Hydra*, etc.), and *Micractinium* (fig. 2, B), whose free-floating cells bear long delicate bristles. Many are colonial, *e.g.*, *Scenedesmus* (fig. 1, D), the flat plates of *Pediastrum* with marginal cells produced into short processes, and the "water-net" (*Hydrodictyon*, fig. 2, C).

The ULOTRICHAELES include unbranched filamentous forms, such as *Ulothrix* (fig. 1, F), not uncommon in streams, and *Hormidium*, forming a weft on damp soil, both with a curved parietal chloroplast in their cells, as well as *Prasiola* which is terrestrial and has an axile chloroplast. The filaments of the last commonly undergo extensive division by longitudinal walls, resulting in leafy expanses which may be very abundant where organic matter abounds (*e.g.*, near the penguin rookeries in the Antarctic). Somewhat similar are the flat sheets of the sea lettuce (*Ulva*) which are common objects on the sea-shore; but here the chloroplast is parietal. The Cladophoraceae, which are usually branched, have large cells containing many nuclei and for this reason are often referred to the Siphonales. *Cladophora*, with thick cell-walls and an elaborate net-like chloroplast is abundant in well aerated pools and streams, and also occurs on rocks in the sea.

In the CHAETOPHORAELES the thallus is differentiated into prostrate and projecting systems, well seen in *Stigeoclonium* (fig. 2, D), where, as often in this group, the branches terminate in long hairs. *Draparnaldia*, which like *Stigeoclonium* is frequent in slow-moving waters, differs in possessing distinct main axes with large clear cells having a scanty chloroplast, while the bunched laterals are deep green. *Trentepohlia*, found as orange tufts on rocks and trees especially in hilly country, has its cell-sap coloured by haematochrome and possesses special zoosporangia. The group also includes many prostrate epiphytes, *e.g.*, *Aphanochaete* (frequent on *Cladophora* or *Oedogonium*) which is markedly anisogamous, and *Coleochaete* (fig. 2, E), whose cells bear curious sheathed hairs and which is oogamous. The common unicellular *Pleurococcus*, found on tree-trunks, etc., is probably an extremely reduced member of this group.

The OEDOGONIALES with big cells containing a netlike chloroplast, reproduce abundantly by large zoospores which bear a ring of numerous cilia and are formed singly in the cells. They include the unbranched *Oedogonium* and the richly branched *Bulbochaete*, where each cell bears a long hair with an inflated base. These are oogamous forms, often producing their flat antheridia in special "dwarf-male" filaments which are found attached on (fig. 1, M) or near the swollen oogonia.

The CONJUGATAE, which are widely distributed in freshwater, are distinguished by their elaborate chloroplasts with prominent pyrenoids, by lacking asexual reproduction, and by a peculiar sexual process (conjugation) in which the gametes are constituted by the contents of the ordinary cells. They comprise a filamentous series (Zygnemales), including *Spirogyra* (with spiral chloroplasts) (fig. 2, F) and *Zygnema* (with two star-shaped chloroplasts in each cell); but are more extensively represented by the unicellular Desmids. The cells of the latter exhibit a great variety of beautiful and symmetrical shapes, and are commonly divided by a median constriction into two semicells, each harbouring one or two complex chloroplasts; examples are furnished by *Closterium* with semilunar cells, *Cosmarium* (fig. 2, G), and *Staurostrum* (fig. 2, I), where the semicells are produced in two or more arms. A few Desmids form threadlike colonies. During conjugation in the Zygnemales, opposite cells of two parallel threads become connected by tubes (fig. 2, F), whereupon the protoplasm of the one glides over into that of the other and fuses with it to form a zygospore (*Spirogyra*), or the protoplasmic masses meet in the tube and form the zygospore there (often in *Zygnema*). In Desmids the protoplasts escape from two adjacent individuals and fuse to form a zygospore which lies between the empty halves of the parent cells (fig. 2, H). Both Oedogoniales and Conjugatae are highly specialized.

The SIPHONALES are coenocytic, *i.e.*, their large multinucleate bodies possess few or no septa. The only freshwater form, *Vaucheria*, shows this clearly, its branched, rather coarse filaments containing numerous nuclei and lens-shaped chloroplasts in the lin-



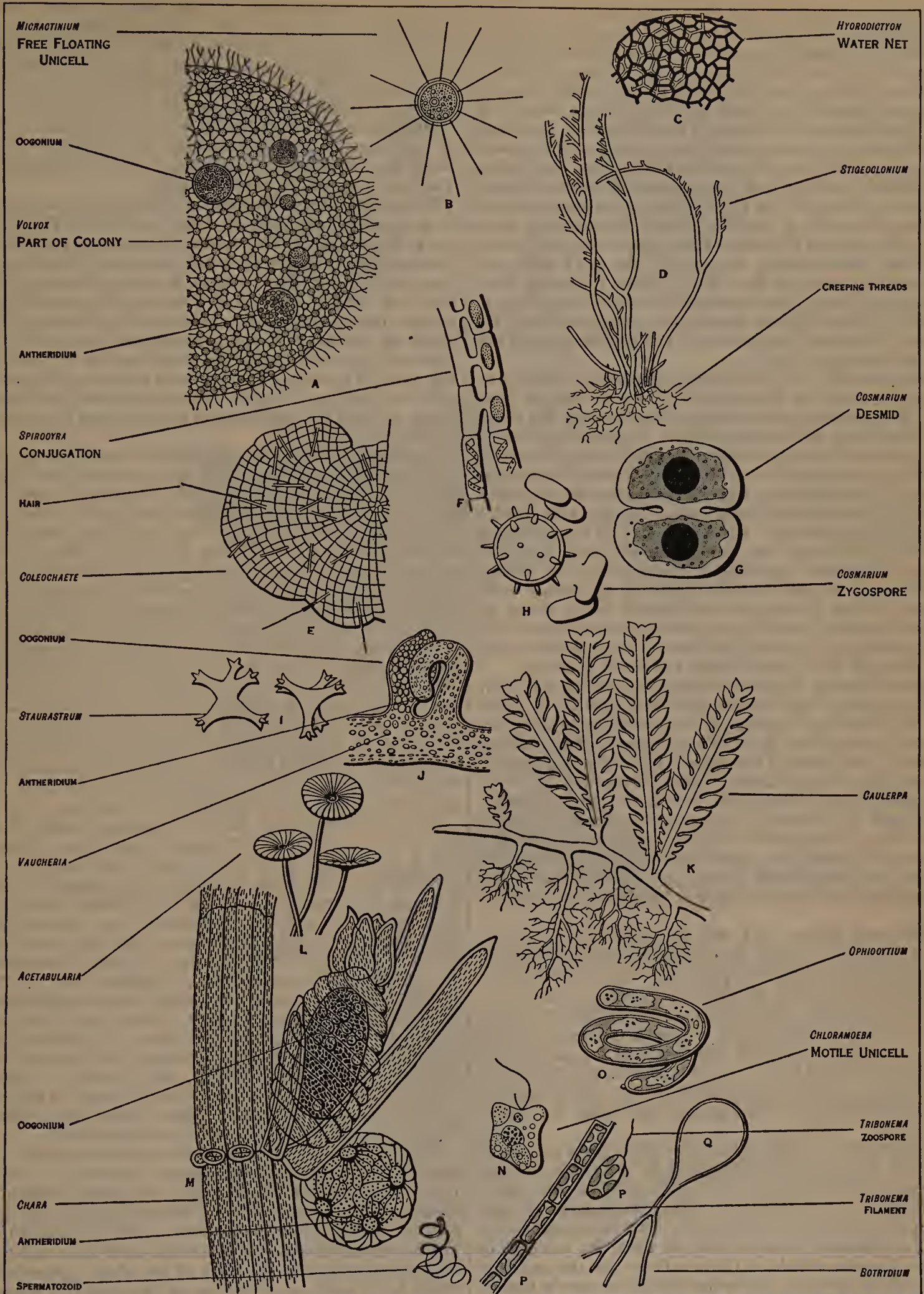


FIG. 2.—THE GREEN AND YELLOW-GREEN FORMS, THE MORE COMMON FRESHWATER AND TERRESTRIAL ALGAE  
 A-F, H-J, D-R FROM WEST AND FRITSCH, "BRITISH FRESHWATER ALGAE," BY PERMISSION OF CAMBRIDGE UNIVERSITY PRESS. G FROM COOKE, "BRITISH FRESHWATER ALGAE," BY PERMISSION OF KEGAN PAUL, TRENCH, TRUBNER AND CO. K, L, AND N FROM ENGLER AND PRANTL, "PFLANZENFAMILIEN," BY PERMISSION OF WILHELM ENGELMANN. M FROM OLTMANN, "MORPHOLOGIE U. BIOLOGIE D. ALGEN," BY PERMISSION OF GUSTAV FISCHER. ALL EXCEPT C, L AND M CONSIDERABLY MAGNIFIED

FIG. 2.—THE GREEN AND YELLOW-GREEN FORMS, THE MORE COMMON FRESHWATER AND TERRESTRIAL ALGAE

The chief groups of Algae are distinguished by the pigments they contain. The Green Algae are the simplest having no other pigment than the green chlorophyll. Green Algae are mainly freshwater or

terrestrial and are recognized by their dark green colour and storage of starch. The Yellow-green Algae, mainly found in freshwater, are distinguished by absence of starch and storage of oil



ing protoplasm which surrounds a huge and continuous vacuole. The marine forms mostly show a more elaborate structure. Thus, the *Caulerpas* of warmer seas have a thallus differentiated into a creeping stem (up to a foot long) anchored by branched rootlets and bearing leaflike outgrowths, which in their varied form and arrangement simulate the shoots of diverse higher plants (fig. 2, κ). Other Siphonales (Codiaceae) resemble certain brown and red seaweeds in having a body built up of numerous closely placed and often intertwined threads like those of *Vaucheria*, e.g., *Codium* and *Halimeda*, the latter with a flat segmented thallus encrusted with lime. In another family (Dasycladaceae) an erect main axis bears compact whorls of branches between which there is often extensive deposition of carbonate of lime; one of the most striking forms is the Mediterranean *Acetabularia* (fig. 2, λ), where the whole plant is encased in lime. Many similar calcareous forms are known as fossils. The Siphonales are mostly isogamous or anisogamous, producing their gametes in special gametangia; but *Vaucheria* is oogamous with antheridia and oogonia situated side by side on the filament (fig. 2, j).

**Stoneworts.**—II. The CHARALES (stoneworts), which grow submerged in fresh and brackish waters, are so complex, especially in their reproductive organs, that they can have but a very remote relationship with the green algae. The slender cylindrical axes bear whorls of short branches (often called leaves), which are separated by long internodes and produce occasional branches in their axils. The popular name is due to the considerable deposition of lime in the superficial membranes. All the cells contain numerous small chloroplasts. The segments cut off from the apical cell divide into an upper half forming a node and a lower half forming an internode; the latter lengthens greatly but remains undivided, while the node becomes segmented by vertical walls, the peripheral cells growing out into "leaves" which, except for their limited growth, show the same structure as the "stems." In *Chara* threads sprout out from the lowest nodes of the leaves and closely invest the stem, but in *Nitella* this cortex is lacking.

In spite of prolific vegetative reproduction sexual organs are formed abundantly. They usually arise close together at a node (fig. 2, μ). The large oogonia are completely invested by five green spiral threads whose tips form a symmetrical group (corona) at the apex. The spherical antheridium has a wall composed of eight somewhat curved "shields" which at maturity acquire a yellow or red colour; to the middle of the inner (concave) surface of each shield is attached a rod-shaped manubrium carrying a number of long coiled threads, in each compartment of which a spermatozoid is formed. At maturity the whole structure falls to pieces and the spermatozooids are set free. The fertilized ovum acquires a thick wall and rests prior to its germination, which is complex.

**Yellow-green Algae.**—III. The HETEROKONTAE are mainly found in freshwater, though the unicellular *Halosphaera* is of widespread occurrence in marine plankton. They are distinguished by the yellow-green colour, the absence of starch, and the storage of oil. The chloroplasts contain much xanthophyll (blue with nitric acid), are commonly disc-shaped, and never possess pyrenoids. The motile stages are provided with two very unequal cilia attached at the front end (fig. 2, ν). The cell-walls are often rich in pectic substances. Sexual reproduction is rare and always isogamous, and both zoospores and gametes are formed in the ordinary cells.

The Heterokontae, though represented by far fewer genera and species than the Isokontae, exhibit much the same range of form. The motile unicell is illustrated by the rare *Chloramoeba* (fig. 2, ν), whose cells are without a wall, but there are no motile colonies. Various palmelloid types are known, the commonest being *Botryococcus*, an abundant plankton form, in which the mucilage of the rather irregular colonies is often so dense that the contained cells are difficult to detect. Motionless unicells are seen in *Chlorobotrys* (a rare moorland form), *Halosphaera*, and the multinucleate *Ophiocytium* (fig. 2, ο), which is common in stagnant pools. Its curved cells have a wall composed of two very unequal pieces, the smaller becoming detached as a lid when zoospores or aplano-spores are to be liberated. *Tribonema* (= *Conferva*, fig. 2, ρ),

a common freshwater form, has filaments with long narrow cells which have a wall composed of two overlapping pieces and many disc-shaped yellowish green chloroplasts. The only siphonous form is *Botrydium* (fig. 2, q), not uncommon on damp mud; when the latter dries, all the protoplasm withdraws into the underground rhizoid and divides into a number of thick-walled cysts.

**Diatoms.**—IV. BACILLARIALES, which are abundant in all kinds of situations, are a specialized class of unicellular and colonial forms whose silicified wall is composed of two overlapping pieces. They are dealt with in a separate article.

**Brown Seaweeds.**—V. PHAEOPHYCEAE (brown seaweeds) are more especially characteristic of the colder seas. Their colour is due to fucoxanthin which accompanies the usual pigments in the chromatophores; there are generally several of the latter of varied shape in each cell. The products of photosynthesis are fucosan (red with vanillin dissolved in concentrated hydrochloric acid) and fat; opinions differ as to the nature of the former. The zoospores are formed in special sporangia and, except in the most advanced oogamous forms, the sexual organs are multicellular (fig. 1, η). The zoospores and gametes have two cilia attached to one side of the body, one directed forwards, the other backwards (fig. 3, β); near the attachment of the cilia there is a conspicuous eye-spot.

The simplest Phaeophyceae are the ECTOCARPALES, the palmelloid forms previously included in this class being now referred to the Chrysophyceae (see PROTOPHYTA). *Ectocarpus*, whose brown tufts or tresses are commonly seen in rock-pools, is like a brown *Stigeoclonium* having prostrate and projecting systems; each branch of the latter grows by the division of a series of flat cells situated below the terminal hair (fig. 1, η). Numerous zoospores (fig. 3, β) are produced in large (unilocular) sporangia (fig. 3, α), while the gametes which are quite similar arise singly in the compartments of elongate gametangia (plurilocular sporangia, fig. 1, η). In *Pilayella* sporangia and gametangia are interspersed between the ordinary cells. The gametes, though alike in form, may differ in behaviour, some soon ceasing to move and being sought out by others which retain their activity. In *Giffordia*, with two kinds of gametangia, there is marked anisogamy. The sexual individuals of *Pilayella* (see *Life-cycle*, p. 592) are found in spring, the asexual in summer; both bear plurilocular sporangia, those of the latter liberating zoospores which give rise to a new asexual generation without the intervention of a sexual one.

Many Ectocarpales are far more complex, though all can be related to *Ectocarpus*. A few examples must suffice. *Desmarestia* (fig. 3, c) has main axes, from 1½–4 feet long, bearing numerous short stiff branches which in winter and spring end in feathery tufts, but in summer are bare. The large cells of the axis (fig. 3, d) each produce a pair of short branches, from the lowest cells of which threads grow out in profusion and become matted together to form a wide "cortex" which grows very thick in the older parts. The branched gelatinous threads of *Castagnea* and the irregular jellylike lumps of *Leathesia*, common on larger seaweeds, are built up of numerous filaments in dense juxtaposition at the surface, but more loosely arranged in the interior. Of a different type are the bladderlike thalli of *Asperococcus* and the long occasionally constricted tubes of *Scytosiphon*, which arise by longitudinal division in the cells of the primary thread followed by the development of a central air-cavity. Many Ectocarpales (*Elachista*, *Myriotrichia*) form small epiphytic cushions or tufts.

The cylindrical threads of the SPHACELARIALES possess a prominent apical cell which cuts off segments parallel to its base (fig. 1, ι). These, without further elongation, divide abundantly and often very regularly by transverse and longitudinal walls; the older parts are, however, often covered by a dense small-celled cortex. The numerous branches mostly remain quite short and by their arrangement determine the habit of the plant. *Sphacelaria* is a bushy form, rarely exceeding one or two inches in height with feathery arrangement of the branches. *Cladostephus* is larger and has whorled branches. The former multiplies abundantly by means of triangular or three-armed propagules. The reproduction of Sphacelariales resembles that of Ectocarpales; some are anisogamous like *Giffordia*.





A AND J FROM ENGLER AND PRANTL, "PFLANZENFAMILIEN," BY PERMISSION OF WILHELM ENGELMANN. B-I FROM OLTMANN, "MORPHOLOGIE U. BIOLOGIE D. ALGEN," BY PERMISSION OF GUSTAV FISCHER. K AND L FROM FRITSCH AND SALISBURY, "AN INTRODUCTION TO THE STRUCTURE AND REPRODUCTION OF PLANTS," BY PERMISSION OF G. BELL AND SONS, LTD. ALL EXCEPT C, F AND G CONSIDERABLY MAGNIFIED

FIG. 3.—BROWN ALGAE, MORE ESPECIALLY CHARACTERISTIC OF THE COLDER SEAS

The Brown Algae have a yellowish to brown pigment in addition to the chlorophyll, which gives them various shades from olive to yellow and brown. There are a dozen or more orders in this group, the

largest of which are the Ectocarpales which consist of very simple forms of filaments, the Laminariales or kelps, and the Fucales which include rock weeds and Sargassum



*Cutleria*, the principal genus of CUTLERIALES has a branched ribbon-like thallus, several layers of cells thick, the ultimate segments ending in a fringe of hairs, each exhibiting at its base a dividing zone like that of *Ectocarpus*. The dark dots on the unisexual thalli correspond to groups of hairs bearing gametangia (fig. 3, E), the female having large deep brown compartments, the male small pale yellow ones. Both gametes are motile (fig. 1, o). After fusion they produce a flat crustlike thallus (*Aglaozonias*-stage, fig. 3, F), several layers of cells thick and bearing a dense row of sporangia on the upper surface. The zoospores ordinarily give rise to the *Cutleria*-plant, but this regular alternation does not always occur, either generation being capable of reproducing itself.

**Oogamous Forms.**—The remaining brown seaweeds are oogamous. Among these the LAMINARIALES alone possess zoospores which are produced in densely crowded sporangia occupying the surfaces of the blades. This group includes the largest seaweeds, which are often very elaborate in form and structure. One of the simplest is *Chorda filum*, whose unbranched whiplike thalli may be several yards long, whilst barely a quarter of an inch thick. In *Laminaria* there is a long stalk terminated by a blade which is entire (*L. saccharina*) or divided into fingerlike segments (e.g., *L. digitata*, fig. 1, K). New blades arise periodically by a gradual widening at the top of the stalk, the old blade being slowly destroyed by the waves. The divided blades of *Laminaria digitata*, etc., arise by the formation in the new growth of several long slits which ultimately reach the free edge. This explains the development of such an elaborate form as *Lessonia* (fig. 3, G), the young stages of which resemble a *Laminaria* with a simple blade; by progressive splitting and the development of separate stalks to the segments the large treelike growth (10–12 ft. high) ultimately arises. *Macrocystis*, the giant of the southern seas, develops in much the same way. Here the slender stalk, which is up to 60 yd. long, trails out from its attachment to the rocks to the surface of the water, where it bears two long rows of narrow blades, floating with the help of air-bladders at their base. *Nereocystis*, which is like a huge *Laminaria digitata* and occurs on the Pacific shores of America, has an immense air-bladder at the top of the stalk. *Alaria*, a much smaller form whose blade has a midrib, has narrow outgrowths on the stalk to which the sporangia are confined. Similarly, in *Macrocystis* the latter are found on simple shoots arising from the base of the stalk.

The complex internal structure has already been described; of special interest are the sieve-tubes, closely resembling those of higher plants, found in the inner cortex of *Macrocystis* and *Nereocystis*. The medulla in all cases contains numerous "trumpet-hyphae" (fig. 3, I) with a marked dilation at the septa which show a sievelike pitting.

The gametophytes are microscopic filaments bearing either antheridia producing a single, almost colourless, spermatozoid (fig. 3, H), or oogonia with a single ovum.

*Dictyota*, which is typical of the DICTYOTALES, has a forked band-shaped thallus growing by an apical cell. The asexual individuals bear at intervals spherical sporangia, each producing four motionless spores. These give rise to male or female individuals. Oogonia and antheridia are formed in compact groups on the surface, the former (fig. 3, J) unicellular and producing each one ovum, the latter of the usual septate type; the male cells have only a single apical cilium. In *Padina*, which is rarer, the thalli are fan-shaped with an inrolled margin and exhibit a prominent concentric zoning.

The FUCALES, although not nearly so large, are quite as complex as the Laminariales. There is no asexual propagation, but sexual reproduction is very prolific. The sexual organs are borne amidst numerous hairs on the inner surface of round cavities (conceptacles) (fig. 3, K), which appear as swellings on the thalli and open to the exterior by a small aperture. The large oogonia (fig. 1, N) produce eight (*Fucus*), four (*Ascophyllum*), two (*Pelvetia*), or only one ovum (*Himanthalia*), while the antheridia, borne in large numbers on branched hairs (fig. 3, L), form minute spermatozooids. Male and female organs occur on distinct individuals or, more rarely (*Pelvetia*) in the same conceptacle. The gametes

are extruded from the conceptacles in a drop of mucilage during low tide, and fertilization takes place when the sea returns. The fertilized ovum grows direct into a new plant. The conceptacles are generally restricted to the tips, although *Fucus* and others have similar, but smaller, barren conceptacles scattered over the whole thallus.

In the bladderwrack (*Fucus*) the flat segments have a thick midrib which persists as a stalk in the older parts of the plant; several species have paired air-bladders. *Pelvetia*, which is much smaller, has narrow branches which are deeply channelled, while the irregularly swollen tips render fertile plants very conspicuous. The long straplike thalli of *Ascophyllum*, dilated at intervals by air-bladders, bear numerous short branches which arise from marginal slits and in the upper parts of the plant contain the conceptacles. In *Himanthalia* the thallus is roughly of the shape of a top and about an inch across, but periodically the upper surface gives rise to a forked straplike outgrowth, as much as a yard long and studded with conceptacles. The distribution of these forms on the sea-shore is dealt with below. *Sargassum* (fig. 1, L) has already been described. The internal structure of Fucales is similar to that of Laminariales, though somewhat simpler.

A seventh group of brown algae, the Tilopteridales, are rare and too incompletely known to be considered here.

**Red Seaweeds.**—VI. RHODOPHYCEAE (red seaweeds) are a highly specialized class, mainly confined to the sea. The marine forms are usually coloured various shades of red or purple, while the freshwater ones are often bluish. The chromatophores, of which several are found in each cell, contain a red (phycoerythrin) and a blue (phycocyanin) accessory pigment, and the different colours are due to the varied proportions in which these two pigments occur. Pyrenoidlike bodies are frequently found in the less specialized forms. The product of photosynthesis consists of small doubly refractive granules of Floridean starch (brownish or reddish with iodine). The thick, mucilaginous cell-walls are usually provided with conspicuous pits connecting the protoplasm of adjacent cells. No red seaweed has any motile reproductive cells.

The simple BANGIALES, whose cells have an axile star-shaped chromatophore and are without pits, include *Bangia*, with unbranched threads whose cells are longitudinally divided, and *Porphyra*, with a flat *Ulva*-like thallus, both marine. Their relation to other red algae is not clear. They reproduce asexually by liberation of the contents (monospores) of ordinary cells, while their sexual reproduction is not unlike that of the Nemalionales (see below).

The large remainder of the red algae, styled FLORIDEAE, are classed in four groups distinguished by the events following upon fertilization. Their thallus exhibits diverse structure, but growth is usually apical. *Callithamnion*, one of the simplest forms, consists merely of richly branched threads with elongate cells. Many other Florideae are filamentous, though with a more elaborate structure. Thus in *Ceramium* the threads show a characteristic banding (fig. 4, D), due to the formation of a small-celled cortex around the upper end of each principal cell. In *Polysiphonia* the segments of the apical cell divide with great regularity by longitudinal walls, forming characteristic tiers with a deeply coloured central cell shimmering through the peripheral ones. *Batrachospermum*, the "frog-spawn alga," found in slowly moving streams, has soft threads resembling a string of beads, each constituted by a whorl of branches (fig. 4, A); the large cells of the main axes are overgrown by cortical threads.

In *Nemalion* or *Furcellaria* the threads are coarser and, like *Codium* or *Castagnea*, composed of numerous filaments in more or less dense aggregation (fig. 1, J). *Corallina* shows the same structure, but here the pink barrel-shaped segments are densely encrusted with lime and separated by uncalcified joints, where the central threads bear no lateral branches. Closely related are *Lithothamnion* and *Melobesia*, with strongly calcified encrusting thalli which are specially common in the warmer seas and often assist in the building of coral-reefs. Such forms are also known as fossils.

Many Florideae have a flattened thallus which may be exten-





A-C, G, N, I FROM OLTMANN, "MORPHOLOGIE U. BIOLOGIE D. ALGEN," BY PERMISSION OF GUSTAV FISCHER. D AND F FROM FRITSCH AND SALISBURY, "AN INTRODUCTION TO THE STRUCTURE AND REPRODUCTION OF PLANTS," BY PERMISSION OF G. BELL AND SONS, LTD. E AND O FROM ENGLER AND PRANTL, "PFLANZENFAMILIEN," BY PERMISSION OF WILHELM ENGELMANN. J-N FROM WEST AND FRITSCH, "BRITISH FRESHWATER ALGAE," BY PERMISSION OF CAMBRIDGE UNIVERSITY PRESS. ALL EXCEPT A, F AND C MAGNIFIED

FIG. 4.—TYPES OF MARINE RED ALGAE AND OF BLUE-GREEN FRESHWATER ALGAE

The Red Algae have a red pigment in addition to the chlorophyll; this gives to their graceful and often delicate bodies beautiful tints and shades of red and purple. They are regarded as the most beautiful of all the marine algae. The Blue-green Algae are a very distinct class,

probably an ancient group that has retained primitive characteristics. Their prevalent colour is blue-green, but other tints, such as violet and red are not uncommon. They are of wide distribution, especially in freshwater and terrestrial habitats



sively branched, e.g., carrageen (*Chondrus crispus*, fig. 4, F) and *Gigartina*, the latter with numerous teatlike outgrowths which harbour the fruits. Some of the most beautiful forms belong to *Delesseria* (fig. 4, G).

**Reproduction of Red Seaweeds.**—The sexual organs are usually formed on the lateral branches, the rounded antheridia in groups, and the female organs (carpogonia) singly (fig. 4, B). Each carpogonium is flask-shaped and prolonged into a narrow neck (trichogyne), the ovum occupying the swollen base. Each antheridium produces a single motionless spermatium, which is conveyed by chance currents to the trichogyne. After solution of the wall the contents of the spermatium pass through the trichogyne to fuse with the female cell. The consequences of fertilization vary in the different groups.

In the NEMALIONALES (incl. *Batrachospermum* and *Nemalion*) numerous short sporogenous threads sprout from the carpogonium (cf. fig. 4, A'), their end-cells liberating naked carpospores which produce a new individual. These sporogenous threads are sometimes regarded as a sporophyte (see above). Asexual reproduction in the Nemalionales is either lacking or effected by monospores formed singly in spherical sporangia.

The remaining Florideae reproduce asexually by tetraspores developed in tetrasporangia which either project freely (fig. 4, C), or, more commonly, are embedded among the superficial cells of the thallus (fig. 4, D); they are sometimes confined to special branches. The tetrasporangia usually occur on individuals devoid of sexual organs, although in other respects similar to the sexual plants. A regular alternation of the two has been established in a considerable number of cases (cf. above).

In the more advanced groups the fertilized carpogonium develops filamentous outgrowths (gonimoblasts, fig. 4, H) which fuse with one or more auxiliary cells distinguished by rich protoplasmic content. At the points of fusion there arise bunches of sporogenous threads forming the carpospores, which produce the individuals bearing tetraspores. Only the protoplasm of gonimoblast and auxiliary cell fuse, their nuclei remaining far apart, so that the process gives rather the impression of a parasitism of the gonimoblast on the auxiliary cell than of a second process of fertilization. In the CRYPTONEMIALES the two or three gonimoblasts are long threads fusing repeatedly with auxiliary cells which are here located at the ends of neighbouring branches (fig. 4, H). In the remaining groups (GIGARTINALES, RHODYMENIALES) the auxiliary cells are associated with the carpogonia to form so-called procarps, and the gonimoblasts are quite short. Thus, in *Callithamnion*, there are two auxiliary cells flanking a cell of the main axis (fig. 4, I, a and b) and one bears the four-celled branch which ends in the carpogonium; two masses of carpospores are formed. In *Polysiphonia* and many other cases the single auxiliary cell and the carpogonial branch become enclosed, already prior to fertilization, by a cuplike outgrowth from the adjacent cells (fig. 4, E). The enlarged envelope subsequently forms an investment around the single mass of carpospores, the whole structure being termed a cystocarp. In forms with a compact thallus the cystocarps are often embedded in the surface layers (fig. 4, F). *Corallina* and its allies produce all their reproductive organs in flask-shaped cavities (conceptacles).

**Blue-green Algae.**—VII. MYXOPHYCEAE (CYANOPHYCEAE) are a very distinct class distinguished by their simple cell-structure, the absence of all motile stages, and the lack of sexuality. They are probably an ancient group which has retained primitive characteristics, and enjoy a very wide distribution, especially in freshwater and terrestrial habitats. The prevalent colour is blue-green, but other tints (violet, red, etc.) are not uncommon. The pigments (chlorophyll, yellow carotin, blue phycocyanin, and a red one similar to the phycoerythrin of red algae) are simply lodged in the peripheral protoplasm, there being no definite chromatophore. The central protoplasm (central body) is colourless and perhaps constitutes a rudimentary nucleus, quite unlike that of other plants. Its structure has been repeatedly investigated, but has not yet found an interpretation that meets with common consent. The products of photosynthesis are sugars and glycogen, the latter causing the brown colouration of the cells after treat-

ment with iodine. The cells often contain numerous granules, some of which consist of protein (cyanophycin granules). The cell-wall is frequently not sharply defined.

The simpler members are colonial and grouped as CHROOCOC-CALES, most of which are palmelloid with the cells embedded in abundant soft mucus (e.g., *Gloeocapsa*, fig. 1, E); they form jelly-like masses on damp walls, rocks, etc. A different type is seen in *Merismopedia* (fig. 4, J) whose plates of deep blue cells are common in freshwater plankton.

The remaining Myxophyceae are filamentous (HORMOGONEALES). *Oscillatoria*, forming vivid blue sheets at the bottom of ponds in autumn, has simple threads (fig. 4, K), which may glide slowly through the water or exhibit slow pendulumlike movements to which the genus owes its name. Many of its allies have their threads encased in a firm mucilage sheath (e.g., *Lyngbya*). In *Phormidium* huge numbers of threads are agglutinated by their soft sheaths to form leathery or papery sheets which often cover rocks, etc., over considerable stretches. In *Scytonema* (fig. 4, N) the filament breaks at certain points and the two pieces push out of the sheath sideways to form paired branches. This "false branching" is common in a number of Myxophyceae. The threads of *Scytonema* and its allies exhibit occasional larger cells (*heterocysts*), which have a firm cellulose wall and whose contents are at first yellow, but ultimately disappear completely.

Heterocysts are also found in the unbranched filaments of *Nostoc* (fig. 4, L) and *Anabaena* (fig. 4, M). The coiled threads of the former are embedded in large numbers in soft mucilage to form spheres or leafy expanses on damp ground or in water. In *Rivularia* and its allies the heterocysts are always situated at one end of the filament, whilst the opposite one tapers to a point or ends in a long hair. *Stigonema* (fig. 4, O) is a more robust form with several rows of cells within the sheath and showing true branching.

In a very few cases the contents of heterocysts have been found to produce a new thread, but for the most part they do not fulfil any recognizable function. Reproduction in the Myxophyceae is usually accomplished vegetatively, by fission in the colonial forms and by the detachment of short lengths of thread called hormogones in the filamentous types. The hormogones perform slow, gliding movements, whose mechanism is not fully understood. Many Hormogoneales produce resting spores, enlarged thick-walled cells with abundant granules, which may arise from any cell of a thread, though commonly located near a heterocyst (fig. 4, M).

The Myxophyceae, though so simply constructed, are successful in many habitats (e.g., hot springs, the frozen Antarctic lakes) where few other algae (except diatoms) can exist.

## PHYLOGENY

There can be little doubt that algae originated in the water and that they preceded in their evolution the more elaborate land-plants. The different classes, as well as some prevalently flagellate groups dealt with elsewhere (see PROTOPHYTES), are distinguished by special pigments in the chromatophores and by the products of photosynthesis. Each class thus has its distinctive metabolism and probably represents the outcome of a separate attempt at the creation of a holophytic organism. There is little evidence of any real relationship between the diverse classes, and a common ancestry is in the light of our present knowledge improbable. In several classes the ciliated individuals and the motile reproductive cells are of a distinctive and rather uniform stamp, and this fact has led to the practically universal adoption of the view that these algal classes originated from motile unicellular organisms (Flagellates) that gradually lost their power of movement and gave rise to filaments, etc., in the way that has been above indicated. In red and blue-green algae, where no motile stages exist, a like origin from unicellular forms is assumed, though these need not necessarily have ever had the capacity of movement.

One may therefore picture the evolution of algae as having followed a number of separate lines, starting each with its unicellular ancestry and branching out in numerous special directions to develop as colonies, as palmelloid types, as filamentous forms



with diverse elaborations, etc. It is unlikely that these principal categories have ever originated directly from one another. They would rather appear to represent as many different attempts at the building of a body from the unicellular ancestry. It is significant that the same types of plant-body are repeated in different classes, since this indicates a parallelism in the evolution of the latter which has only recently been recognized. In some classes (e.g., Heterokontae) evolution has not progressed far, while in others (e.g., Phaeophyceae and Rhodophyceae where the simpler forms seem to be extinct) it has led to the production of highly specialized types in part of large size.

The biggest range in structure and reproduction is encountered in the green algae, although they have not attained to the complexity or dimensions of the brown and red seaweeds. The absence of the more specialized forms in this very vigorous and adaptable class is possibly due to their having migrated to the land in the remote past, although others hold that the higher plants originated from a hypothetical group of large green seaweeds now altogether extinct, and at least as complex as the brown and red forms of the present day.

### OCCURRENCE AND DISTRIBUTION

**Benthos.**—Most algae grow permanently submerged, and are either attached (benthos) or free-floating (plankton). In freshwaters the algae of the benthos grow on stones, twigs, and larger aquatics, while the benthic seaweeds are nearly all lithophytes (i.e., fixed to rocks). Few algae (*Chara*, *Caulerpa*) can obtain a foothold in loose sand or mud, and a rock on a sandy beach often stands covered with vegetation like an oasis in a desert. Members of the benthos may become detached from their substratum and float freely, like the tangles of filamentous algae found in ponds, or the seaweed *Sargassum*, innumerable plants of which drift into the North Atlantic from the Gulf of Mexico and the Caribbean sea and thus give rise to the Sargasso sea. Unattached species of *Fucus* are not uncommon in salt marshes, but most seaweeds are doomed when torn away from their substratum. In rivers too all algal growth, other than the plankton, is attached, either encrusting rocks and pebbles (Myxophyceae, the red *Hildenbrandtia*) or forming long tresses trailing out with the current (*Cladophora*, *Ulothrix*, various red algae). All benthic forms bear numerous epiphytes and their dense tangles usually harbour a wealth of smaller algae and animal life.

**Zonation.**—The benthos usually exhibits more or less pronounced zoning. In lakes and pools this is due to the gradual diminution in light-intensity with increasing depth of water. The epiphytes on the submerged Phanerogams often show such zoning clearly, while in deeper water the growth consists in the main of Charales, *Nitella* usually thriving at greater depths than *Chara*. Further out, where the light is reduced to a minimum, the bottom bears only diatoms and sometimes cladophoraceous forms. Zonation is much more marked on rocky shores, where the littoral zone (i.e., the region between tide-levels) is of considerable extent. The highest levels are occupied by forms like *Pelvetia*, *Bangia*, *Prasiola*, etc., which are only under water for a few hours or indeed may grow at such a height, as to be merely wetted by spray and submerged only at spring tides. This spray-zone has its equivalent at the margins of large lakes, where the stones bear a growth of *Spirogyra adnata*, Myxophyceae, etc. Below the spray-zone, on northern shores, there follows a broad girdle of *Fucus*, various species of which occupy different levels; in the lower stretches they are mingled with *Ascophyllum*, while near low tide level *Himanthalia*, and Corallinaceae are often conspicuous features. In the sublittoral zone Laminariales are the dominant forms in all the colder seas. In the Mediterranean the littoral zone is specially characterized by *Corallina mediterranea*. Between tide levels are also found many green (*Ulva*, *Cladophora*) and red algae, but the latter, both as species and individuals, are most abundant in deeper water, where they are never exposed.

The various pigments (brown, red, blue, etc.) that accompany the chlorophyll probably serve in the first place to screen the latter against the intense illumination to which seaweeds are exposed when uncovered by the tide. The Rhodophyceae of the

littoral zone usually possess a dark red, almost black colour, and the brighter tints are met with only in the permanently submerged forms. Red seaweeds are, in fact, so sensitive to strong light that in aquaria they have to be grown behind dark glass.

The accessory pigments in the chromatophores, however, also effect an alteration in the region of maximum absorption of light. While in green plants this is in the red part of the spectrum, in the case of red algae it is in the green. So that at considerable depths, where the red and yellow rays have been absorbed, while the green and blue ones are relatively undiminished, red algae can still carry on photosynthesis and will be more successful than green or brown forms. It has been thought that their characteristic colour may have been acquired as a direct response to the quality of the light, but this is a debated point. It is well known, however, that some *Oscillatorias* will take on a colour complementary to that of the light to which they are exposed. Various Myxophyceae that grow in deep water, moreover, assume a red colour. It appears, however, from recent research that other factors than the colour of the light (e.g., lack of nitrogen) may bring about a change of pigmentation.

**Phytoplankton.**—The members of the phytoplankton are largely unicellular or colonial and are often highly adapted to a floating life. Many take the shape of flat plates (e.g., *Pediastrum*, *Merismopedia*, fig. 4, J), others bear numerous bristles (*Micractinium*, fig. 2, B) which heighten their buoyancy, while some (e.g., the many Myxophyceae responsible for "water-blooms") possess structures in their cells (pseudovacuoles) which render them lighter than water. A number of plankton algae (e.g., Volvocales), moreover, are freely motile and can thus maintain themselves in the surface layers where alone they obtain adequate illumination.

Marine phytoplankton consists largely of Diatoms, Peridiniae, and a few Heterokontae (*Halosphaera*, *Meringosphaera*), although a red filamentous member of Myxophyceae (*Trichodesmium*) is sometimes abundant in the warmer seas, hence the name of the Red sea. Freshwater phytoplankton is more diverse, including apart from Diatoms and Peridiniae, many Isokontae and blue-green algae. Since the phytoplankton constitutes the diet of many smaller animals, its abundance is often intimately related to the productivity in fish of oceanic or lacustrine waters. It varies considerably, both in quantity and quality, in different seasons of the year, and there is usually a more or less marked annual succession of forms (Diatoms, Peridiniae, etc.), many of which appear in swarms of rather limited duration.

**Periodicity.**—Such periodicity is also observable in the benthos and may be very striking in ponds, where four or more distinct phases can sometimes be distinguished during the year and certain forms (*Spirogyra*, *Tribonema*, etc.) are commonly only present during a limited period. The flora is usually poorest in the height of summer. Seaweeds likewise exhibit a periodicity, some being annuals and absent in the unfavourable season (winter or summer, as the case may be), whilst others though lasting for two or more years periodically shed parts of the thallus (cf. *Laminaria* and *Desmarestia* above). Reproduction is, moreover, commonly confined to definite periods; thus, many species of *Spirogyra* and *Oedogonium* are found fruiting mainly in spring, *Coleochaete* in the summer, the Laminariales produce their sporangia especially during the winter months, etc. Sexual reproduction in freshwater algae usually occurs during periods of bright sunshine.

**Conditions of Existence.**—The effect of light on the distribution of algae has already been considered. Second in importance is temperature, which probably in large part conditions the broad differences in the composition of the algal flora over the surface of the earth. In the colder seas other seaweeds are overshadowed by the large brown forms (Laminariales, Fucales), which are far less abundant in tropical and subtropical waters where red algae and Siphonales come to the front. Such regional differences are not so marked in freshwaters, although certain forms (*Cladophora*), common in temperate zones, are rare in the tropics, where moreover Myxophyceae play a bigger rôle than in colder latitudes. Some of these differences are no doubt determined by the higher oxygen-content of colder waters.



In extreme temperatures the algal flora acquires a very distinctive stamp. Thus, in hot springs the vegetation consists almost entirely of Myxophyceae and Diatoms, some of which are able to thrive at very high temperatures (80°C and more). Many algae, on the other hand, can withstand low temperatures and may be melted out from ice in a perfectly healthy condition. The frigid Antarctic lakes contain huge sheets of the blue-green *Phormidium* bearing a host of epiphytes. A peculiar flora consisting mainly of green algae occupies the surface of the perpetual snow-fields of the Alps, Andes, etc., and of the polar regions. Over wide areas the snow may exhibit a red colour due in the main to the resting-cells of *Chlamydomonas nivalis*, with which other forms are associated. Yellow snow, with a different flora, occurs in the Antarctic and is also known from the Alps.

Few algae can stand appreciable variations in the concentration of the water. Freshwater forms are not very tolerant of an excess of salts and seaweeds cannot thrive in dilute water, so that in estuaries and on salt-marshes only a limited number of algae are to be found.

**Endophytes and Parasites.**—The majority of epiphytic algae are attached merely to the surface of their substratum, but especially among marine forms some of the threads not uncommonly penetrate the latter, either invading only the external membranes of their host or burrowing deeper, so that they become active parasites. In most cases such forms afford little outward indication of their parasitism, but in the red alga *Harveyella* (*Choreocolax*) *mirabilis* the cushionlike thalli are devoid of all colour. It is rare for algae to be parasitic on higher plants, but *Cephaleuros*, one of the Chaetophorales, attacks the leaves of various tropical Phanerogams (including tea and coffee), causing more or less serious diseases.

A number of algae (*endophytes*) live almost entirely within the interior of other plants, without as a general rule being more than space-parasites. Such are the species of *Chlorochytrium* which occur in the fronds of the duckweed, etc., the *Nostoc* found in the liverwort *Anthoceros*, and the species of *Anabaena* that inhabit *Azolla* and the roots of various higher plants. In other cases the endophyte merely lies within the thick surface membranes of its host (many marine algae). A more intimate relation (*symbiosis*) exists in the case of the "green cells" (*Chlorella* spp.) found within the bodies of various lower animals, and the association of *Trebouxia*, *Trentepohlia*, and certain Myxophyceae with fungi to form lichens. Here the alga receives both protection and food from its partner (animal or fungus), which in turn profits by absorbing some of the products of photosynthesis of the alga.

**Terrestrial Algae.**—Numerous algae can exist more or less successfully out of water. The amphibious seaweeds of the littoral zone form a case in point. Somewhat similarly situated are the forms (*Botrydium*, *Vaucheria*) that grow on the damp mud round the edges of pools and ditches and which form resting spores as soon as the mud dries. There are, however, many algae living in and on soil, which are more highly adapted to withstand prolonged drying. The subterranean community comprises green (*Chlorococcum*) and blue-green forms, as well as diatoms, cultivated soils in general having a richer flora than natural ones. There can be no doubt that these algae fulfil an important rôle in the soil. A capacity to fix atmospheric nitrogen has been attributed to them, but no decisive proof is yet forthcoming. The gelatinous sheaths of many soil-algae, especially Myxophyceae, may well serve as a home and as a source of carbohydrate-supply for nitrogen-fixing bacteria, and herein may lie their chief importance.

The numerous subaerial algae are mainly green and blue-green, the latter playing a dominant part in the warmer humid regions of the world, where they constitute important primary colonizers of rock-surfaces and may often cover the latter for many hundreds of square yards with sheets of distinctive tint, giving a characteristic coloration to the landscape. In temperate regions green terrestrial algae are more conspicuous. Every one will be familiar with the green covering on tree-trunks, etc., due to *Pleurococcus* and other unicellular forms, which possess such a capacity to resist desiccation that they will survive months of extreme

drying in a desiccator over concentrated sulphuric acid without harm. Other examples of green subaerial algae are *Zygonium ericetorum*, one of the Conjugatae whose purple or greenish wefts cover extensive tracts of peaty soil, *Hormidium* found on clayey soils, and *Trentepohlia* whose orange tufts are particularly common in hilly districts and in the damp tropics. All these can survive long periods of drought without any appreciable change, resuming growth as soon as wet weather sets in.

**Geographical Distribution.**—While the broad differences in the character of the algal flora in diverse situations and in different regions of the earth are without difficulty related to special factors, the analysis of the conditions that determine local variations is still in its infancy. Such variations are patent to any one who makes a study of the algae of a limited region. Thus the algal flora of a moorland pool differs from that of one situated in meadow land, that of a lake differs according as the bottom is rocky or covered with silt, calcareous waters are poor in algal growth, etc. Similarly the vegetation of the sea-shore varies with the nature of the rocks, the extent of wave-action, the presence of currents, and the amount of detritus borne by the waves. Other differences appear to depend rather on geographical than on ecological factors. Thus, the desmid flora has a distinctive character in different parts of the world, and desmids appear to be entirely absent from the Antarctic continent, though abundant in the Arctic. Similar observations may be made with reference to the geographical distribution of seaweeds.

**Uses.**—Relatively few algae are of economic importance. Seaweeds are in many places employed as a convenient form of manure. A species of *Porphyra* (*P. laciniata*) and the red seaweed *Rhodomenia palmata* are used as food in some places, the latter being known as dulse. Agar-agar, a substitute for gelatine, is derived from a species of *Gracilaria*, while another red seaweed, carrageen (*Chondrus crispus*), has been used as an invalid food. Iodine was at one time mainly obtained from the ash of seaweeds.

**Fossil Algae.**—The dense incrustation of carbonate of lime found in various Siphonales and in the Corallinaceae has already been mentioned, and very similar forms are known as fossils in the Trias as well as in the Palaeozoic from the Silurian onwards. Such algae have evidently contributed to no small extent to the building of limestones, just as the *Lithothamnions*, etc. (Nullipores) are important agents in the formation of coral-reefs at the present day. Algae, which are not thus encrusted, are not so readily preserved as fossils, and of such we have little more than a fairly reliable record of their presence in earliest times; some of the forms in question are of large dimensions (e.g., the Devonian *Nematophycus*) and may have been similar to Laminariales. For fossil diatoms, see BACILLARIALES.

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**BAST**, the common name for the outer part (phloem) of the vascular bundle of a plant. The term is also applied to piassaba fibre, etc.



**BIENNIALS**, the name applied to plants which normally complete their life-cycle in two years. They usually devote the first year to the laying up of a store of food, and the second to flowering. This period is not, however, always fixed, as if food is scarce the plant may delay flowering for a longer period than one year, or may flower in the first year as in the bolting of such a plant as the beet.

**DECIDUOUS**, a botanical and zoological term for "falling in season," as of petals after flowering, leaves in autumn, the teeth or horns of animals, or the wings of insects.

**FUNGI**, a large group of plants devoid of green colouring matter (chlorophyll) and reproduced by spores. They include many of the lowest forms of plant life. The thallus is unicellular or composed of branched tubes or filaments which have apical growth. The spore may consist of one or many cells. The absence of chlorophyll has a striking effect on the mode of life of fungi since in its absence they are unable to synthesise carbohydrates from the carbon dioxide of the air. They are dependent therefore on other plants or animals for their supplies of carbohydrates and sometimes of organic compounds of nitrogen. These supplies are obtained from living organisms by parasitic fungi, or more commonly from their dead remains by fungi which are termed saprophytes. Certain non-chlorophyllous organisms however are separated from the fungi and regarded as independent groups.

The fungi are a large group distributed over the whole world wherever other living organisms are found on which they may depend for their subsistence. The number of species is very large; probably 100,000 is a conservative estimate, but no figures,

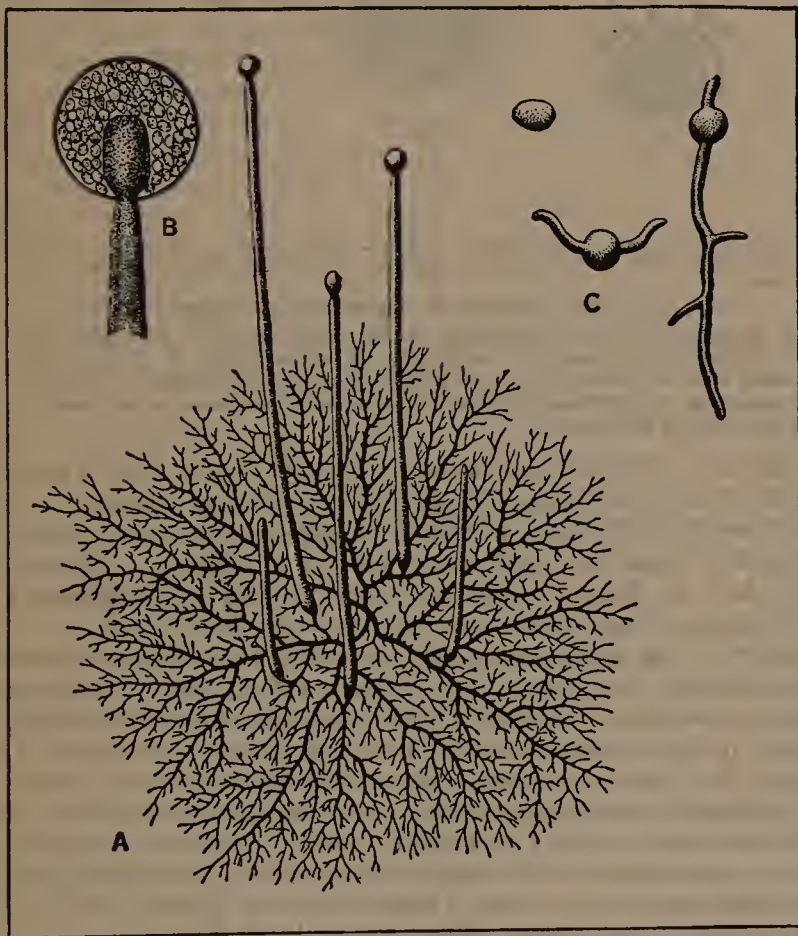


FIG. 1.—A. MYCELIUM. B. SPORE. C. GERM TUBES

however carefully compiled, can be other than provisional. The bulk of the species known belong to the temperate zone. A wealth of forms no doubt exists in the tropics which have yet to be discovered. Geologically the fungi are an old group; the delicate nature of their tissues has militated against their preservation as fossils, but the hyphae of parasitic fungi are found in some of the earliest plant fossils known to us, the beautifully preserved remains of the Rhynie chert of Devonian age.

**Organization.**—If spores of common white mould (*Mucor*) are placed in a suitable food-solution they readily germinate; they absorb water and swell—the dark outer coat (exospore) ruptures and the thin colourless inner coat (endospore) protrudes

and lengthens to form a short tube, known as the germ tube (fig. 1 c). This tube grows at its tip and lengthens considerably; branches arise from it, elongate and branch in their turn and so give rise to an interconnected series of tubular structures known as hyphae. Each hypha is covered externally by a membrane and encloses a mass of protoplasm in which many nuclei are embedded. In older hyphae vacuoles appear and coalesce to form a large central vacuole. Through the walls of the hyphae food solutions are absorbed which provide for their further growth and extension. The whole system of hyphae thus represents the vegetative body of the fungus known as the mycelium (fig. 1 a). As the development of the mycelium proceeds the work of absorption becomes restricted to the younger hyphae which are growing forward into fresh areas of the substratum. The protoplasm of the older parts of the mycelium becomes stored with reserve food-materials and sooner or later from this part of the mycelium arises a new kind of hypha, devoted to the reproduction of the mould. These hyphae are stouter, limited in growth and with a different reaction to such stimuli as light, gravity, oxygen, etc. Thus they normally grow upwards into the air, towards the light, and terminate their growth by swelling at the tip to form a spherical head (the sporangium), the contents of which divide into many portions, each of which secretes a wall and becomes a spore (fig. 1 b). The production of sporangia continues while external circumstances remain favourable and while fresh supplies of food material are available to the developing mycelium. Given these conditions there is no reason why growth should ever cease. In the case of the fungi causing the well-known fairy rings, common in pastures, from a comparison of the rate of growth with the size of the ring, it has been estimated that the age of certain rings is not less than 3–400 years. Although the actively growing hyphae of *Mucor* are continuous tubes with numerous nuclei in their protoplasm and are hence described as caenocytic, the older hyphae show numerous cross walls which serve to cut off useless side-branches and to concentrate the food-reserves. In the majority of fungi all the hyphae are segmented (multicellular), the segments being multinucleate or more commonly with one or two nuclei.

The cell walls of certain groups of fungi (*Saprolegniaceae* and *Peronosporaceae*) give the same reactions as those of the higher plants and apparently consist of cellulose, but Gilson and Van Wisselingh have shown that in a very large number of forms the main constituent of the wall is chitin, a substance common in many animals, e.g. insects. In many cases the membranes undergo secondary changes and other substances may be added such as resins and colouring matters, the walls may become thickened by the deposition of new layers and often profoundly altered by lignification and suberization (*Fomes*, *Daedalea*). A striking change is carbonization, in which the walls become black and brittle.

(*Daldinia*, *Cucurbitaria*).—In the reproductive bodies of many of the higher fungi the walls of certain hyphae become mucilaginous, being hard and horny when dry but capable of absorbing water with great rapidity and consequent swelling. Striking thickening and differentiation may occur in the walls of spores which are commonly pitted, sculptured and ridged.

In the simpler types of mycelium the hyphae show little differentiation except in size. In many parasites in which the hyphae traverse the intercellular spaces of their hosts, lateral branches are produced which penetrate into the living cells and there carry on the absorption of food materials, these haustoria may have the form of simple or branched hyphae or swollen vesicles. In many mycelia the hyphae may become woven together into threads or cords. These may be white and tender as in the "spawn" of the common mushroom, or develop an outer hard and dark coloured layer and so assume a root-like appearance as in the rhizomorphs of the honey fungus, *Armillaria mellea*. In other cases the closely interwoven hyphae may form compact masses, varying in size from that of a pin's head (*Botrytis*) to that of a man's head and weighing 10 to 25 lb. (*Polyporus Myllitae*). These bodies known as sclerotia show also a differentiation into a hard, black outer layer and an inner white core—the whole body consisting of hyphae so closely interwoven and copiously branched and segmented as to resemble in section parenchymatous tissue of one of the higher



plants. From its mode of formation, however, this tissue is more properly described as plectenchyma or pseudo-parenchyma.

Both rhizomorphs and sclerotia serve for the collection and storage of reserve foods to be used in the formation of reproductive bodies, or in the resumption of vegetative activity. The former also serve to extend the fungus and in some parasites act as organs of attack (*Armillaria*).

In the higher fungi a similar interweaving and compacting of hyphae are involved in the formation of the fruit bodies or sporophores and in these structures a high degree of elaboration and of differentiation of the plectenchyma may occur (Polyporaceae, Phallaceae fig. 19).

**Cell Contents.**—In addition to the protoplasm and nuclei, the hyphae of fungi may contain, like other vegetable cells, substances of various kinds. Amongst the more easily identified are oil-drops—often coloured—crystals of calcium oxalate, proteid granules and crystalloids and resin. Starch apparently never occurs but glycogen is common and other carbohydrates such as the sugars almost certainly occur in the living cell. Other substances which can be readily extracted from fungal tissues include acids such as oxalic, citric and many other lichen acids, ethereal oils, resins and a number of powerful alkaloid poisons such as ergotin, muscarin, etc. Many of the coloured pigments are fixed in the cell-walls or deposited on their surface (*Chlorosplenium*) but in some cases are dissolved in the oil which occurs in drops in the protoplasm (*Pyronema*, *Monascus*).

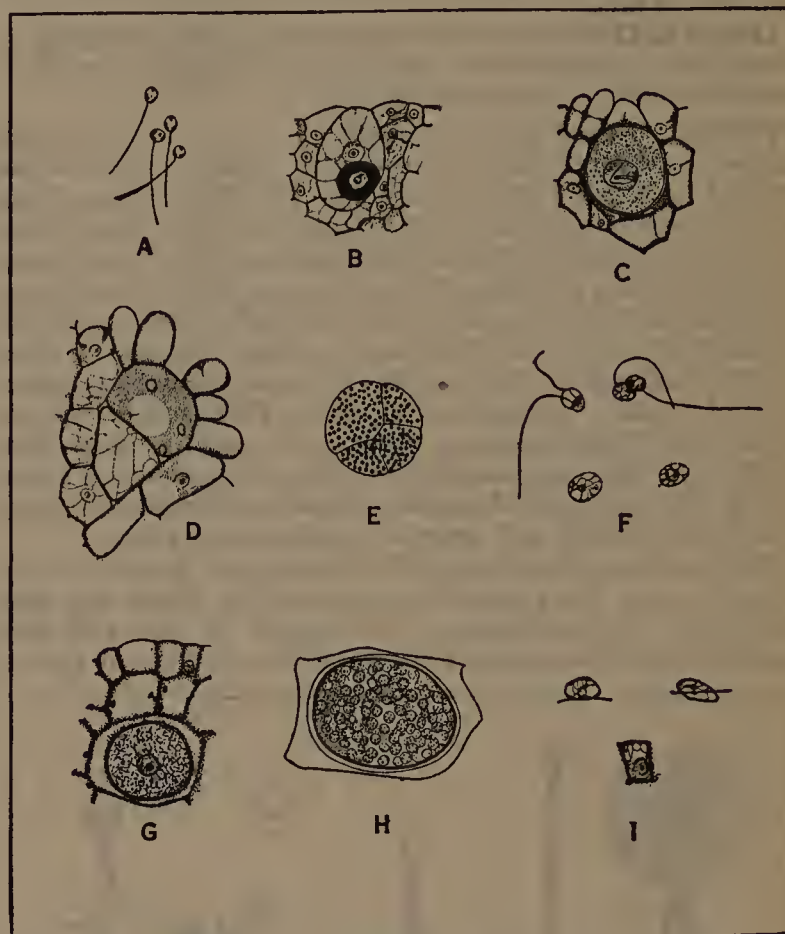
The particular mode of nutrition of the fungi, viz., their dependence on other organisms for their food materials, is only rendered possible by their power of secreting a whole range of ferments capable of digesting the many complex substances which go to form the bodies of plants and animals. Amongst the enzymes extracted from fungi may be mentioned as examples, *diastase* which converts starches into sugar, *cytase* with a similar action on cellulose, *peptase* which converts proteins into peptones and amides, *lipase* which hydrolyses fat and oils, *invertase* which splits cane sugar into simple sugars such as grape sugar, and *zymase* which decomposes grape sugar into alcohol and carbon dioxide. These or similar enzymes are found as normal products of metabolism in plants generally where they play their part in the necessary digestion of reserve foods, etc. Whilst, however, in the higher plants their work is performed with few exceptions in the cells or the tissues in which they arise, in the fungi these ferments are excreted by the hyphae in order to bring about the necessary changes in the food-substance with which they come into contact. All fungi are apparently not capable of secreting every kind of ferment and so are unable to utilize all classes of food materials. Many are restricted in their choice, or rather show special facility in dealing with particular materials, e.g., horn, feathers, cellulose, fats. Some moulds on the other hand (*Penicillium*, *Aspergillus*) can utilize almost any organic food material and a large number of enzymes have in fact been extracted from these forms.

### CYTOLOGY AND REPRODUCTION

Although the small nuclei of certain fungi were not recognized by early investigators, subsequent improvements in methods of research have demonstrated their presence in all the species in which they have been sought. In the lower fungi the hyphae are coenocytic, i.e., they contain numerous nuclei and these are of small size (.001–3 m.m. in the Mucoraceae). In the higher fungi the segments may contain several nuclei (*Pyronema*, *Aspergillus*) but usually have only one or two. There is no reason to doubt that not only are they as essential to the cell of the fungus as to that of any other organism, but that they are fully comparable with those of the higher plants both in essential structure and in function. They normally divide mitotically (see CYTOLOGY) and in a number of cases, where the nuclei are of considerable size, the details of division have been minutely described (*Phyllactinia*, *Humaria*). Typical spindles with centrosomes and asters are formed and the chromosomes are clearly differentiated. The number of chromosomes is usually small, e.g., eight in *Phyllactinia*.

As in the higher plants, in those fungi in which sexual repro-

duction occurs, the essential feature of fertilization is the union of two nuclei. These are, in the simplest cases, the nuclei of the sexual cells or gametes and the new cell which results is known as the zygote. This has a double number of chromosomes, and is therefore described as diploid in contradistinction to the haploid nuclei of the sexual cells and of any vegetative cells associated



FROM "PROCEEDINGS OF THE ROYAL SOCIETY," BY COURTESY OF THE COUNCIL AND K. M. CURTIS

FIG. 2.—LIFE HISTORY OF *SYNCHYTRIUM ENDOBIOTICUM*

A. Zoospores, B. Young protoplast within a hypertrophied epidermal cell, C. Mature summer spore, D. Germination of summer spore, E. Young sorus, future walls indicated by lines, F. Copulation of two planogametes, G. Young hyphospore, H. Hyphospore during maturation of zoospore primordium, I. Penetration of the zygote

with them. Fertilization thus marks the end of one definite phase in the life of the fungus (haploid phase) and the beginning of a new one (diploid phase) of which the zygote is the starting point. This in its turn must end with a process of reduction (meiosis) by which the haploid nuclei are again restored (see CYTOLOGY). Fertilization and meiosis are thus two cardinal points in the history of an organism; ending the haploid and diploid phases respectively. In some of the higher fungi, these alternating nuclear phases are associated and correlated with striking differences in the vegetative structure of the mycelia concerned. In these the zygote may give rise to many generations of diploid cells which eventually produce the mother-cells—usually of special form—in which meiosis will occur. These cells—gonotocysts—correspond to the spore-mother-cells of the higher plants and like them they produce a definite number (four or eight) of daughter-cells, the spores, which contain haploid nuclei.

**Life History of a Simple Fungus.**—Some of the essential facts referred to above may be illustrated by reference to the life history of one of the simplest of the lower fungi, *Synchronium endobioticum*, a parasite on potato tubers where it causes the well-known and destructive wart disease. The parasite enters an epidermal cell of the potato as a small naked protoplast containing a single nucleus. It increases in size at the expense of the contents of the host cells and, when these are exhausted, its vegetative activity is brought to an end. It now surrounds itself with a wall of two layers, a thicker outer exospore and a thinner endospore and becomes a summer spore (fig. 2 c). The exospore then ruptures and allows the endospore (prosorus), still enclosing the protoplasts, to escape into the host cell. Here the nucleus



begins to divide and by successive divisions, a number of nuclei, usually 32, are formed. The whole contents now become divided into several (five to seven) portions each of which becomes surrounded by a separate wall. We have thus formed a group of cells in which as many as 300 nuclei may be formed by further division and the whole protoplasmic contents become cleft into as many small naked spores each containing a single nucleus. The cells containing these spores (the sporangia) burst and liberate their contents and each spore is seen to be provided with a motile organ in the form of a delicate protoplasmic thread or cilium. By the cilia the spores are able to propel themselves in the soil water and, from this animal-like movement, are known as zoospores. They settle down eventually on the surface of a young tuber, throw off their cilia and then penetrate the outer cell-wall of the host and so effect an entrance to the interior of the cell. Here they repeat the development described above. Thus the haploid generation of *Synchytrium* can reproduce itself and the cycle of zoospore-vegetative-cell-summer-spore-sporangia-zoospore can be many times repeated. The release of the zoospores from the ripe sporangia is dependent on the presence of free water. If their escape is delayed for a time they show a significant difference in behaviour. They swim towards other zoospores, they fuse together in pairs and the fusion cells, now provided with two cilia, after independent movement, settle down and infect the cells of the host (fig. 2 f, g). As many sporangia will liberate their contents simultaneously when wetted, it is probable that any two cells uniting together will be derived from different sporangia. The zoospores in this case behave as sexual cells or gametes; there is no morphological difference; a zoospore is a potential gamete and its behaviour is determined by physiological conditions. The young zygote contains two nuclei which fuse and form a diploid nucleus. In the host cell it enlarges and on the exhaustion of available food surrounds itself with a double wall. So far its development resembles that of a haploid plant, but it now shows a marked difference in behaviour, since it passes into a resting condition, which may persist until the next spring. It is therefore known as a resting spore (fig. 2 i). Eventually the nucleus divides and it is probable that there is a true meiotic or reduction division. After repeated divisions, zoospores are formed and set free by the splitting of the thick wall. Thus the haploid generation again begins its development. Here, then, we have the nuclear cycle completed, and the haploid and diploid phases are each associated with a distinct generation of the fungus which, though resembling one another in vegetative structure, differ in the final products of their development. The haploid generation is terminated by the production of gametes and their conjugation; the diploid generation is terminated by meiosis and the resulting production of haploid zoospores.

**Fertilization.**—The conjugation of two similar gametes (isogamy) is characteristic only of the simpler fungi. Throughout the whole group it is possible to trace tendencies, which have not only profoundly modified the type of sexual reproduction, but in so doing have directly contributed to the success of the fungi in their transition from an aquatic to a terrestrial mode of life. These tendencies have led to the suppression of the individualization of the gametes and the assumption of their functions by the gametangia—the structures in which gametes are formed.

In the simplest cases this has resulted in the sexual process consisting in the fusion of two entire individuals. These are usually of different size and we can distinguish a smaller male and a larger female (*Polyphagus*, fig. 3 d). The mature individuals thus form a single gametangium and the distinction of sex is marked by calling the male gametangium an antheridium and the female an oogonium.

In most fungi the whole plant is not involved in reproduction as in *Synchytrium* and *Polyphagus*, but only certain hyphae which bear the gametangia. Thus many gametangia are borne on each individual and here we can distinguish two possibilities. The individual may bear gametangia of both kinds (monoecious, hermaphrodite, bisexual) or there may be two kinds of plants each bearing one kind of gametangium only (dioecious, unisexual). Since in the fungi we have only to consider sex in relation to the

haploid generation, it is more convenient to distinguish these fungi by the terms first suggested by Blakeslee for the Mucoraceae—homothallic (monoecious) and heterothallic (dioecious). Thus *Polyphagus* is heterothallic.

In the Mucoraceae in which both types of thallus occur, the gametangia, which contain a large number of nuclei representing the potential gametes, show no morphological distinctions into antheridium and oogonium. When they fuse their contents are mingled and a large number of nuclei pair together; we thus have multiple fertilization which, however, only results in the production of one zygote, a coenozygote.

In the Oomycetes, homothallism is the rule (except *Dictyuchus*), and the gametangia are clearly differentiated into antheridia and oogonia. In *Monoblepharis* the antheridia give rise to a number of uniciliate male gametes which are set free in the water to find the oogonium. The latter's contents round off to form one large naked uninucleate mass termed the oosphere or egg (fig. 4 a). This is not strictly a gamete, since it represents the whole contents of the gametangium and at first contains many nuclei—potential gametes. In other members of this group (*Saprolegnia*-ceae, *Peronosporaceae*) the element of chance in fertilization is still further reduced. The antheridia are brought into contact with the oogonia and the male gametes—now undifferentiated and represented only by their nuclei—are brought directly into contact with the eggs (fig. 4 d, e). As in the Mucoraceae, these fungi are independent of water for fertilization. It is this independence of water both for fertilization and, as will be shown later, for the dissemination of spores, that has rendered possible the migration of fungi from a life in water to an existence on land and on land plants.

In the higher fungi a further modification can be traced which leads to the suppression of the function of the male organ and finally to its disappearance. This does not involve the absence of fertilization, but the fusion of nuclei derived from nearly related cells of the female organ (*Ascobolus*) or of nuclei within the common mother-cell (*Humaria*, *Lachnea*). This leads finally to the disappearance of the female sexual organs and a condition of pseudogamy in which the cells concerned are two vegetative cells sexually different but not differentiated in structure. This is the case, e.g., in many yeasts and in some of the higher Basidiomycetes. These fusions of vegetative cells may appear to be on all fours with the anastomoses which occur not uncommonly between ordinary vegetative hyphae, but that they differ in kind is clear from the fact that they have the essential character of a sexual fusion inasmuch as they form the starting point of new development. As in all types of fertilization they mark the beginning of the diploid generation. A reference to the conditions existing in *Synchytrium*, where every zoospore is a potential gamete, may help the realization, that in a haploid or gametophyte generation of one of the higher fungi, however numerous the cells or diverse in structure, every nucleus has the same organization, every cell has the potentialities of a sexual cell.

**Asexual Reproduction.**—The reproductive bodies of fungi are known as spores. The simplest type of reproduction is the separation of a cell or group of cells which is capable of independent growth and which thus serves to propagate the fungus. Although physiologically these behave as spores they are usually distinguished as oidia (*Monilia*) or, in sprouting fungi such as the yeasts, as buds or gemmae. From a morphological standpoint spores are marked off from the hyphae which produce them by their form, size, colour, mode and place of origin, etc. Spores formed within a special sac, the sporangium, are known as sporangiospores, or if motile as zoospores. If they are cut off terminally from a hypha they are conidia and the parent hypha is a conidiophore. Chlamydospores are thick-walled, usually resting spores formed like conidia or more usually as intercalated bodies on ordinary hyphae. The various kinds of spores of fungi also receive special names in the different groups, and these, although given without any reference to general principles, are useful and convenient owing to their descriptive character.

**Sporophores and Fruit Bodies.**—In the simplest cases, the spore-bearing structures or sporophores are hyphae which by their



form and behaviour are marked off from the rest of the mycelium. They are simple or branched in a definite manner, they grow up into the air or radiate into the surrounding water. They may be isolated but are frequently associated together. If they are united into bundles these are called coremia; if in flat layers, sporodochia. They are often borne on a plectenchymatous cushion known as a stroma, and are distributed over its whole surface. In other cases the plectenchyma forms a hollow body which bears the conidia on its inner walls. These structures are termed pycnidia and their conidia are usually distinguished as pycnospores.

The various spore forms referred to above—sporangiospores, conidia, etc., are sometimes described as "summer" spores. It is a somewhat misleading term, but it does indicate that these bodies serve the purpose of rapid propagation of the fungus under favourable conditions. They are produced for the most part on haploid mycelia and appear as soon as the necessary food-materials have been accumulated by the vegetative hyphae. In the higher fungi special types of fruit bodies occur which are distinguished by the fact that they consist wholly or in part of diploid hyphae and that they are concerned with the production of gonotoconts, those cells in which the reduction divisions are effected. The gonotoconts produce daughter cells—the spores—with haploid nuclei. Where the spores are produced within the mother-cell—endogenously—it is called an ascus and the daughter cells ascospores. Where they are borne externally—exogenously—they are termed basidiospores and the mother cell a basidium. Details of the structure and mode of formation of these fruit bodies will be given in later sections dealing with classification (*see below*, Ascomycetes and Basidiomycetes).

#### PHYSIOLOGY

The general physiology of the fungi does not differ essentially from that of other plants. Their requirements are the same as those of the living cells devoid of chlorophyll of the higher plants, wherever these may occur. Like them they require water, various inorganic salts and supplies of carbonaceous and nitrogenous foods in varying degrees of complexity. They respire, taking in free oxygen and liberating free carbon dioxide or excreting carbonic acid. Aerial hyphae transpire and often exude drops of water; waste products (*e.g.*, calcium oxalate) are also excreted. They respond to external stimuli such as light, gravity, certain chemical substances, etc.

The one fact which dominates and restricts the mode of life and nutrition of the fungi is the absence of chlorophyll and their consequent dependence on outside supplies of organic carbon and in many cases of organic nitrogen. Fungi are therefore compelled to live on materials derived from other plants or from animals, and are either parasites on living organisms or saprophytes living on their dead remains. No hard and fast line can be drawn between these habits. There are many fungi normally living as parasites which can exist as saprophytes and vice versa. The large majority of fungi are saprophytes and they, with the bacteria, are the great agents of decay in nature. The vast amount of vegetable material which annually falls to the soil, the remains of herbs, the fallen leaves of deciduous trees, the fallen branches and trunks of forest giants, the excrement and the dead bodies of animals are all material for the sustenance of fungi. They are abundant in the upper layers of the soil in which these organic remains become incorporated by the action of many animals, *e.g.*, worms, beetles, etc. In the household they are found on stale foods of every kind, on preserves, on damp clothing and leather, wall paper and plaster. Special means are therefore taken to protect foods from destruction by the common moulds.

**Harmful Forms.**—The preservation of food such as fruit, meat, etc., is effected by first sterilizing the material by heat, which destroys active mycelia and spores, and secondly by preventing the access of other air-borne spores. Thus bottled fruit is heated to a temperature of 160° F, which destroys the yeasts and other fungi on the surface of the fruit, and the bottles or tins are closed whilst the space above the liquid in the tin or bottle is filled with steam. The same method of procedure is adopted for the preservation of meat but the food is raised to a higher

temperature. The preservation of jams depends not only on the sterilization by heat during their preparation, but on the high percentage of sugar, incorporated with the fruit, which is unfavourable to the development of mycelia and of yeasts. Where moist air is allowed access, by imperfect covers or bad conditions of storage, to the surface of the jam, water may be absorbed by the sugar and the concentration sufficiently reduced to allow moulds to develop. The damage is therefore confined to the surface layers. Where the proportion of sugar is low, yeasts may enter and cause fermentation, indicated by bubbles of gas and a pronounced alcoholic flavour.

Great damage is often caused to floor-boards, wooden partitions and wall-panelling by wood-destroying fungi, notably by the dry rot fungus, *Merulius lachrymans*. This attacks both soft and hard woods, its mycelium destroying the cell walls, reducing the wood to a soft brownish mass which as it dries becomes characteristically fissured by right-angled cracks. When the surface of the wood is dry the mycelium is largely confined to the inner layers, but in a moist atmosphere the mycelium appears on the surface of the wood, forming continuous sheets of tissue and giving rise to numerous strands and cords which pass to neighbouring wooden structures. Under these circumstances the spread of the fungus and the consequent destruction of the wood is rapid and unchecked. The cords enormously extend the range of the fungus; they have been known to spread along the surface of brick walls, to penetrate the mortar between the bricks and so convey the destroyer from one room to another. There is little doubt that the fungus is in most cases introduced with the wood, but the extent of the resulting damage can be minimised by ensuring that wood used in construction is dry and well seasoned and thoroughly ventilated. As a preventive against the attack of this and other fungi, wood is often treated with tar, creosote and other fungicides. (*See DRY ROT.*) The consumption of wood in coal mines is enormously increased by the short life of the pit props, whose decay is promoted by the warm humid atmosphere so favourable to the rapid development of mycelia.

**Symbiosis.**—The living together in close association of two dissimilar organisms is described as symbiosis and the fungi afford some of the best known instances of this mode of life. Lichens form a classical example. In these dual organisms a fungus and an alga are associated together. Both components derive advantages from the association. The alga receives from the fungus water and inorganic substances and in some cases is protected from desiccation; it grows and increases by vegetative means. The fungus is, however, the dominant partner. It derives its organic food supplies from the alga and in many cases has been observed to send haustoria into the alga cells. It alone produces a fructification. (*See LICHENS.*) The parasitic fungi provide another group of examples in which, however, the relation between the symbionts is definitely antagonistic. (*See PLANT PATHOLOGY.*)

There exists, however, another association between fungi and the higher plants in the formations which are known as mycorrhizas. These are structures in which a fungus is found growing in intimate relation with the roots of one of the higher plants. They are widespread, occurring, *e.g.*, in the common forest trees of the temperate zone (Cupuliferae, Coniferae), in the heather and other members of the Ericaceae, in many orchids and in a large number of other plants which live in soils rich in humus. On the forest trees the mycorrhizas can be distinguished by their frequently branched coralloid appearance, and the presence of a complete mantle of fungal hyphae covering the terminal portion of the root. In orchids and in members of the Ericaceae another type is found, in which the fungus is for the most part inside certain of the living cells of the root and sometimes of other members. These two different types of mycorrhiza have been distinguished as ectotrophic and endotrophic. These terms are convenient to distinguish extreme cases, but intermediate forms are not unusual. As to the fungi concerned, a large number of the higher fungi (Hymenomycetes, Gasteromycetes) have been stated to be concerned in the formation of the mycorrhizas of forest trees. They are not usually specific and not only may a number of different fungi form mycorrhizas on one and the same



species of tree, e.g., the beech, but these in many cases show quite distinct differences in form, colour, etc. In the case of many orchids, the fungi concerned are nearly related and have been referred to the genus *Rhizoctonia*.

The whole question of the significance of these structures and of the relations existing between the fungus and its host, has provided a wide field for speculation and in recent years has led to experimental investigations which have yielded important and suggestive results. On the whole, these investigations may be said to support the view that these structures are of benefit to the host plant. It does not follow that any obligate relation exists between the fungus and the host. In the case of forest trees seedlings can be grown successfully in the absence of the fungus, but there is strong evidence that the presence of the fungus may promote the absorption of nitrogenous substances from the humus of acid soils and this may well be a decisive factor in the success of trees established in such conditions. In the case of many orchids whose seeds are notoriously difficult to germinate, successful growth can be induced by sowing the seeds on a suitable medium containing the appropriate endophytic fungus. Even here, however, the same results can be obtained in the absence of the fungus by a careful adjustment of the composition of the medium. Interesting as these latter results may be, as indicating the possible rôle of the fungus in promoting germination, it can hardly be doubted that in nature the latter plays a decisive part. It is probable that in these plants, and in forest trees, the fungus in the root cortex may serve to assist in the absorption of organic compounds. The strong development of similar fungi in the tissues of those orchids, which are devoid of chlorophyll and must therefore depend for their whole supply of organic food on the humus in which they live, gives strong support to this conclusion. There is no evidence that the plant in these cases is able to undertake this absorption in the absence of the fungus. The presence of fungi, which probably have a similar significance to those of mycorrhizas, has been noted in other groups of plants. They are known to be of regular occurrence in many liverworts, the prothallia of *Lycopodium*, the rhizome of *Psilotum* and in a number of ferns (Ophioglossaceae, Marattiaceae).

**Medicinal and Dietetic Uses.**—Although, in common with many other plants, fungi have played their part in the preparation of various specifics, only one yields a drug of first importance, viz., the ergot, *Claviceps purpurea*. The active principles are the alkaloids, ergotamine and ergotoxine and extracts containing these are used for obstetric purposes. *Boletus laricis* yields a drug long used under the name of agaricus albus.

In addition to these forms, many other fungi contain poisonous substances such as alkaloids which render them extremely dangerous when used as foods (species of *Amanita*, *Stropharia*, *Russula*, *Boletus*, etc. See Plate). However, there are a number of fungi which are perfectly wholesome when properly prepared, and although in England the common mushroom (*Psalliota campestris*) alone is generally eaten, on the continent of Europe many other species are eagerly sought, e.g., *Lepiota procera*, *Morchella esculenta*, *Boletus edulis*, *Cantharellus cibarius*. In addition to these species the truffle (*Tuber*) is universally esteemed a great delicacy.

**Economic Uses.**—The common mushroom is extensively cultivated and finds a ready sale at all seasons. It is sometimes grown on beds of horse manure out of doors, but more usually in special houses or pits, or in caverns or tunnels such as disused quarries. These beds are infected with "spawn" which consists of cakes of manure permeated with the mycelium of the fungus, whose growth has been arrested by drying.

The fungi which are the most important from an economic standpoint are the yeasts. They owe their importance to their power of fermenting various sugars with the production of alcohol (see BREWING). Brewers' yeast is also used in bread-making, the "rising" of the bread being caused by the escape of the bubbles of carbon dioxide evolved by the fermenting yeast. Another fungus, *Mycoderma aceti*, can, in the presence of oxygen, change the alcohol of fermented liquors to acetic acid and so produce vinegars. Of minor importance may be mentioned the species

of *Penicillium* with which various cheeses (Stilton, Gorgonzola) are inoculated in order to produce the characteristic green-veining and improvement in flavour.

## CLASSIFICATION

It has for long been recognised that the fungi proper fall into three main groups, the Phycomycetes, Ascomycetes and Basidiomycetes. The scheme of classification put forward by O. Brefeld and F. Von Tavel has been very generally accepted and has formed the basis of more recent arrangements of the groups. Brefeld's classification of the higher fungi was, however, based on the conception that their characteristic reproductive structures, the ascus and basidium, had been derived by modification from the asexual sporangium and conidiophore respectively, of certain Phycomycetes. With increasing knowledge of the widespread existence of a sexual process in the higher fungi, with the modern developments of cytology, and appreciation of the rôle of the nucleus in fertilization and its importance in genetics, Brefeld's view of the origin of the ascus and basidium can no longer be maintained. These structures are now recognised as the gonotocysts, the cells in which the reduction division is effected and cannot be homologised with the asexual reproduction organs of the haploid mycelium of the Phycomycetes. Although the view has been expressed that the fungi are polyphyletic, i.e., they have arisen from the algae as several distinct groups, each with an independent origin, there is considerable justification for the view that the main advance has been in one monophyletic series and that the higher fungi have originated from the Phycomycetes, though not in the manner postulated by Brefeld. This view will be further discussed in the detailed consideration of the groups.

### Scheme of Classification.

**CLASS I. PHYCOMYCETES.** Thallus a naked protoplast or an unsegmented coenocytic mycelium, sexual reproduction usual.

Order I. *Archimycetes*. Mycelium poorly developed or absent zoospores common, sexual reproduction frequent.

Order II. *Oomycetes*. Mycelium well developed, asexual reproduction by zoospores or conidia, sexual reproduction by oogonia and antheridia, resulting in oospores.

Order III. *Zygomycetes*. Mycelium well developed, asexual reproduction by sporangiospores or conidia, sexual reproduction by conjugation of similar gametangia and production of zygospores.

**CLASS II. ASCOMYCETES.** Thallus a segmented mycelium, segments with one or many nuclei, asexual reproduction common, sexual reproduction of wide occurrence, often much reduced. Characteristic spore-bearing structure the ascus.

Subclass 1. *Protascineae*. Asci free on mycelium.

Orders, *Endomycetales*, *Exoascales*.

Subclass 2. *Euascomycetes*. Asci collected on or within a fruit body. Orders, *Plectascales*, *Perisporiales*, *Hypocreales*, *Sphaeriales*, *Dothideales*, *Hysteriales*, *Phacidiales*, *Pezizales*, *Tuberales*, *Laboulbeniales*.

**CLASS III. BASIDIOMYCETES.** Thallus a segmented mycelium, segments with either one nucleus or with two, asexual reproduction not uncommon, sexual reproduction much reduced. Characteristic spore-bearing structure the basidium.

Subclass 1. *Protobasidiomycetes*, Basidia septate. Orders, *Uredinales*, *Auriculariales*, *Ustilaginales*, *Tremellales*.

Subclass 2. *Autobasidiomycetes*, Basidia aseptate. Orders, *Tulasnellales*, *Dacryomycetales*, *Cantharellales*, *Polyporales*, *Agaricales*, *Plectobasidiales*, *Gasteromycetes*.

**Phycomycetes.**—I. The *Archimycetes*. These parasitic and mainly aquatic forms have been looked upon as degenerate Oomycetes and were formerly included in that group. Simplicity of structure, however, though it is often the result of degradation, is equally a mark of primitive organisation. The fact that in this group is found the simplest type of sexual reproduction known among the fungi is justification for regarding them as an assemblage of primitive organisms, whose relation to the other groups of Phycomycetes is somewhat obscure. The simplest representatives such as *Olpidium* and *Synchytrium* live in the cells of their hosts as naked protoplasts. They reproduce by uniciliate zoospores, which under certain conditions behave as gametes (see above *Synchytrium*). The zygote resulting from the conjugation of the gametes has a period of vegetative growth and encysts to form a resting spore. A similar mode of life and vegetative structure is exhibited by *Olpidiopsis* in which the zoospores are biciliate; here, however, there are no motile gametes, a larger female and a



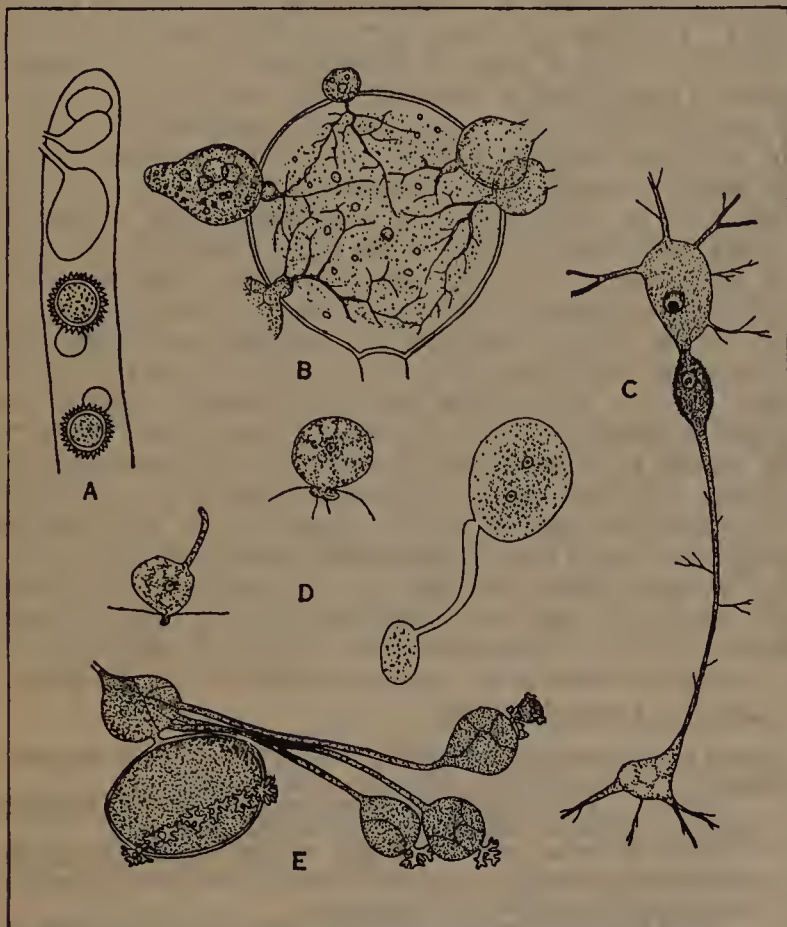
smaller male individual fusing together. These are multinucleate and may be regarded as gametangia which have assumed the functions of gametes (fig. 3 a).

In *Rhizophidium* the parasite is enclosed in a membrane and lives outside its host, into which it sends a short peg-like haustorium, which in some related forms (*Rhizidiomyces*), develops delicate absorbing threads (fig. 3 b). At maturity the whole

sexual organs a series of modifications, which can be directly related to the gradual change of habit from an aquatic to a terrestrial existence.

The lower families are propagated by zoospores, uniciliate in *Monoblepharis*, biciliate in the Saprolegniaceae and Ancylistineae (fig 4 b) borne in sporangia which, e.g., in *Saprolegnia*, are but slightly enlarged terminal portions of the hyphae which bear them. In *Pythium* and *Phytophthora* the sporangia are spherical or oval in form and in certain conditions (absence of free water) they can put out a germ tube and so give rise directly to a hypha. In other genera (*Peronospora*) this direct mode of germination is alone possible, zoospores are no longer produced, the zoosporangium has become a conidium—capable of germinating in moist air and so adapted for a parasitic life on land plants (fig. 4 b).

In their sexual reproduction the group exhibits very strikingly the tendency already mentioned to replace the union of gametes by the fusion of gametangia. In *Monoblepharis* the female organ, the oogonium, contains a single, non-motile, uninucleate egg. It is fertilized by a motile spermatozoid, which closely resembles in structure the zoospores. The zygote resulting surrounds itself with a thick membrane and forms a resting oospore (fig. 4 a). In *Saprolegnia* the young oogonium contains many nuclei, potential gametes, but of these only a few become each the nucleus of an egg, of which there are several in the mature oogonium. There



FROM E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER)

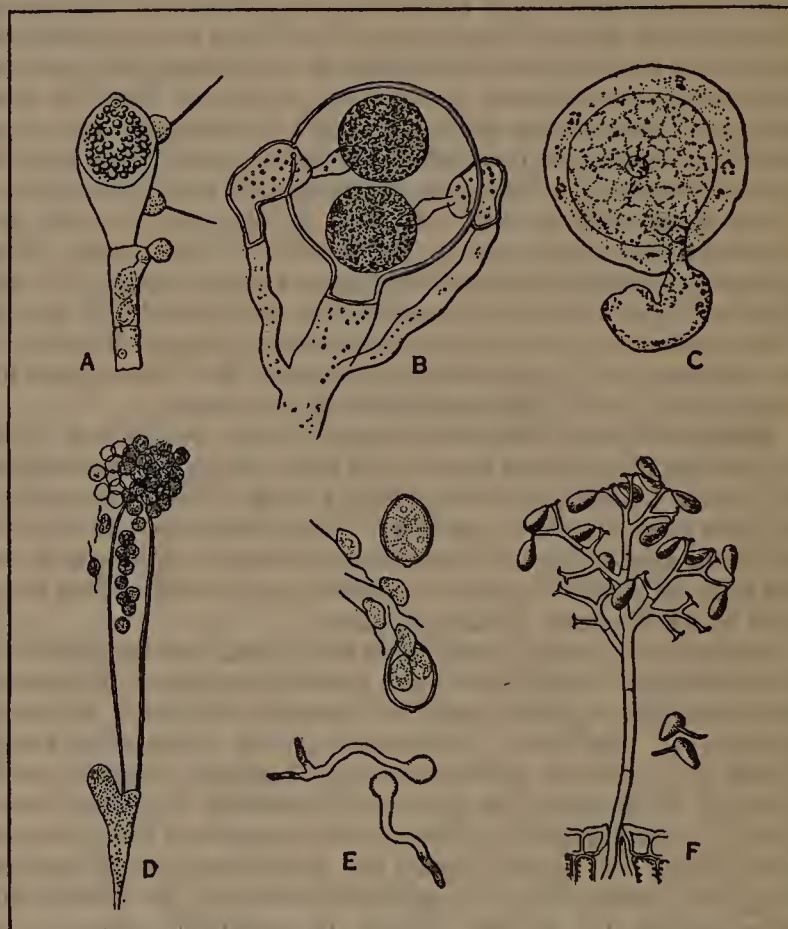
FIG. 3.—A. HOST HYPHA WITH 3 EMPTY ZOOSPORANGIA AND 2 HYPNOSPORES (*OLPIDIUM SAPROLEGNIAE*), B. OOGONIUM OF *SAPROLEGNIA* WITH SPORANGIA IN DIFFERENT STAGES OF DEVELOPMENT (*RHIZIDIOMYCES APOPHYSATUS*), C. YOUNG ZYGOTE, FEMALE NUCLEUS ABOUT TO ENTER COPULATION TUBE (*POLYPHAGUS EUGLENAE*), D. MALE INDIVIDUAL AND COPULATION PROCESS, FEMALE, AND PLASMOGAMY, E. TURBINAT CELL WITH MATURE AND IMMATURE HYPNOSPORES (*UROPHLYCTIS ALFALFAE*)

body becomes a sporangium or acquires a thick wall and forms a resting spore. Sexual reproduction is unknown, but in the related *Zygorhizidium* conjugation between two individuals creates a resting zygote (fig. 3 d). This mode of sexual reproduction in which the conjugation of two individual plants is concerned is found in other forms, e.g., *Sporophlyctis*, *Polyphagus*. In the latter, which is parasitic on *Euglena*, the fungus possesses a highly developed system of hyphal-like haustorial threads, enabling it to attack a number of alga cells simultaneously (fig. 3 c). In other members of the group these threads, though extremely delicate, may be regarded as fine hyphae. In *Physodema* and *Urophlyctis* they develop at intervals large swollen vesicles, the collecting cells, which not only serve as centres for fresh hyphal development, but give rise to large, thick-walled resting spores (fig. 3 e).

*Olpidium Brassicae* causes a disease of cabbage seedlings, the species of *Synchytrium* cause warts or tumour-like swellings on their hosts (e.g., potato, dog's mercury, dandelion) and similar lesions are caused by species of *Urophlyctis* on alfalfa, beet and other plants.

II. The Oomycetes. These fungi have a well developed mycelium of large coenocytic hyphae. The lower families (Monoblepharidaceae, Saprolegniaceae) are saprophytes, living in water on vegetable or animal remains, the Ancylistineae being reduced forms, parasitic on algae, eelworms, etc., the Peronosporaceae are saprophytes or highly specialised parasites on land plants.

The group exhibits in the structure both of its asexual and



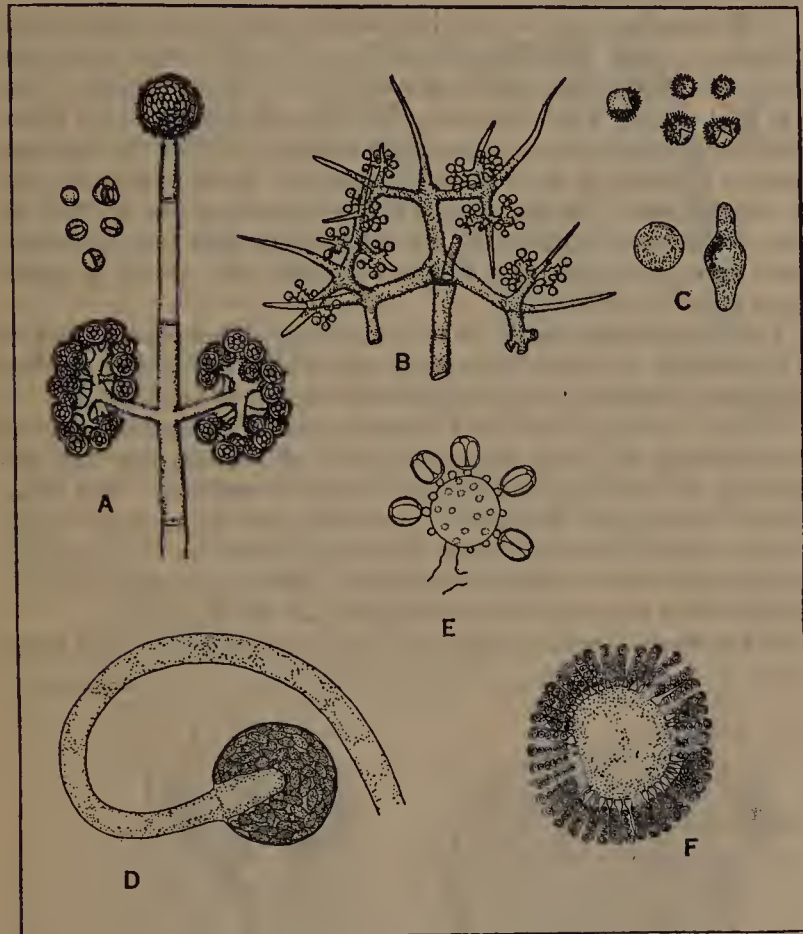
FROM (A) E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER), (B) G. MASSEE, "PLANT DISEASES" (GERALD DUCKWORTH), (C) GWYNNE-VAUGHAN & BARNES, "FUNGI" (CAMBRIDGE UNIVERSITY PRESS)

FIG. 4.—A. FERTILISATION OF *MONOBLEPHARIS MACRANDRA*, B. PROPAGATION BY BICILATE ZOOSPORES IN *SAPROLEGNIA*, C. PLASMOGAMY (*PYTHIUM DEBARYANUM*), D. CELL IN WHICH ARE PRODUCED SWARM-CELLS OR ZOOGONIDIA OF AN *ACHLYA*, E. DEVELOPMENT OF SPORANGIA AND GERMINATION OF ZOOSPORES FORMED IN SPORANGIA IN *PHYTOPHTHORA INFESTANS*, F. A CONIDIOPHORE ENLARGED THROUGH A STOMA OF AN ONION LEAF, AND 2 FREE CONIDIA (RIGHT) OF *PERONOSPORA SCHLEIDENI*

are no spermatozoids, and male gametes are not differentiated, the antheridium puts forth a fertilization tube which conveys the male nuclei to the eggs. Thus, even in members of a family exclusively aquatic, water is no longer the means by which the male gametes reach the eggs. Some members of this family have but one egg in the oogonium and this is the rule in the other families. In *Albugo Bliti* the egg has many nuclei and numerous male nuclei pass from the antheridium and fuse with them. We have thus



multiple fertilizations and the oospore which results may be regarded as a coenozygote since it contains many zygote nuclei, each the result of a separate fertilization. In most of the higher Oomycetes however the mature egg is uninucleate and only one male nucleus passes into it from the fertilization tube. Thus the final result of the assumption of the function of the gametes by the gametangia is a single fertilization, made, however, under such conditions as to eliminate accidents and ensure the production of the zygote.



FROM (A, B, C, E, F) E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER), (D) AFTER F. MOREAU IN "LE BOTANISTE"

FIG. 5.—THAMNIDIUM ELEGANS. A. TERMINAL SPORANGIUM AND SPORANGIOLES. B. CONIDIOPHORE WITH CONIDIA. C. GERMINATION OF SPORANGIA WITH SINGLE SPORES. D. BLAKESLEA TRISPORA, ORIGINAL FORM OF SPORANGIA. E. FORMATION OF EXOGENOUS SPORANGIOLES. F. SYNCEPHALASTRUM CINEREUM, DEVELOPMENT OF EXTRASPORANGIAL PARTIAL SPORANGIA

Many of this family are dangerous parasites of cultivated plants and the cause of destructive diseases, e.g. "damping off" disease of seedlings (*Pythium*), potato disease (*Phytophthora*), vine mildew (*Plasmopara*).

III. The Zygomycetes. These fungi are largely saprophytic in habit and terrestrial. Their mycelium resembles in structure that of the Oomycetes. Zoospores are unknown, the characteristic reproductive organs of the leading family, the Mucoraceae, being sporangia which may contain (*Mucor*) thousands of spores (fig. 1 b). Certain genera, however, are reproduced by conidia, e.g., *Chaetocladium*, *Cunninghamella*, and there are a series of forms which show that in this family, as in the Oomycetes, a transformation of sporangia to conidia has taken place. In one series this has been brought about by the gradual reduction in the number of spores in the sporangium; so, e.g., *Thamnidium* has small sporangia with two to four or sometimes only one spore and *Chaetocladium* may be regarded as a genus in which the small sporangia each contain a single spore and hence behave as conidia (fig. 5 a, b, c).

In another series, *Blakeslea* produces sporangia of normal type and also spherical heads bearing a number of small sporangia with only 3 spores. These can be related to the spherical conidiophores of *Cunninghamella* and *Syncephalis*.

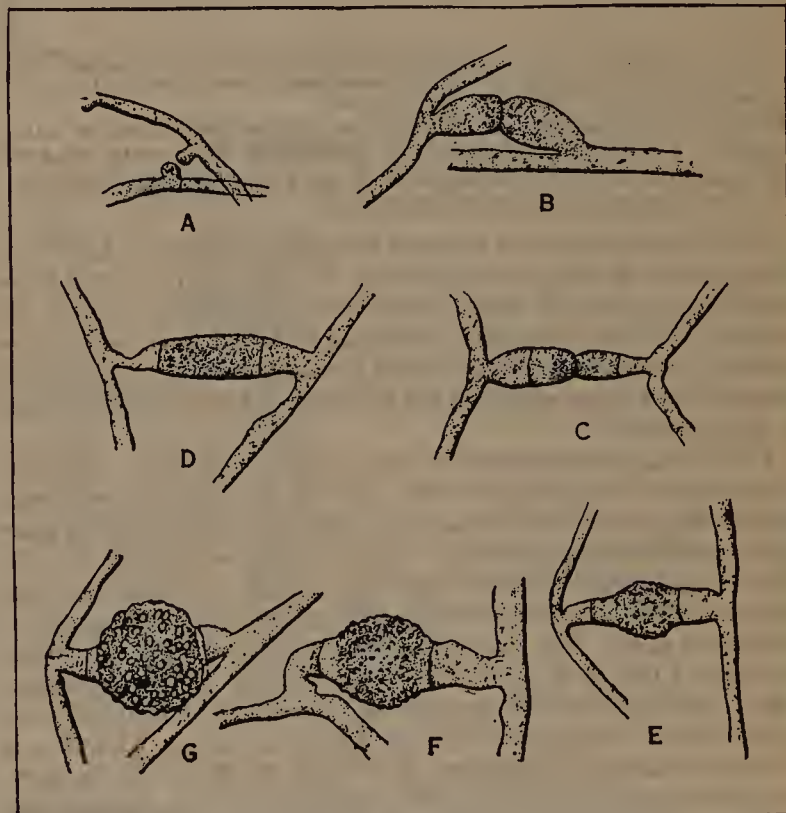
In their sexual reproduction the Mucoraceae exhibit the conjugation of coenocytic gametangia, the resulting structure, the zygospore, containing many zygote nuclei. The gametangia con-

cerned may arise on the same mycelium, on a common supporting hypha or zygomphore as in *Sporodinia*, *Zygorhynchus*, and such forms are described as homothallic. In the majority of the species so far investigated the gametangia arise on two separate mycelia, which are different in kind. There is little doubt that these two kinds of mycelium represent distinct sexes. A. F. Blakeslee, to whom the discovery of this condition—known as heterothallism—is due, pointed out that a difference of vigour, indicated, e.g., by a greater luxuriance of growth, was often to be observed between the two strains, which for this reason he distinguished as (+) and (−). He was able to show, moreover, by the production of so-called hybrid reactions that there is an essential sameness in all the (+) and in all the (−) strains, respectively, throughout the family, and that the (+) strains are probably to be regarded as female and the (−) as male.

The germination of the zygospore usually results in the production of a "germ" sporangium and in *Phycomyces nitens* it is in this structure that the zygote nuclei undergo the reduction division. The resulting spores are in the main of two kinds, producing (+) and (−) mycelia respectively; but there are also a few spores which give rise to feeble thalli—neutral mycelia—which are homothallic. It is of interest to note that H. Burgeff experimentally produced similar mycelia by the admixture of the contents of hyphae from (+) and (−) mycelia, and thus reached the conclusion that homothallic mycelia contain both (+) and (−) nuclei.

The Entomophthoraceae is a family of insect parasites of which one, *Empusa muscae*, attacks the common house-fly. They are reproduced asexually by conidia which are shot off from the conidiophores and form a halo around the dead flies.

The small family of the Endogonaceae with a single genus *Endogone* may be included here. The species form mostly under-



FROM GWYNNE-VAUGHAN AND BARNES' "FUNGI" (CAMBRIDGE UNIVERSITY PRESS)

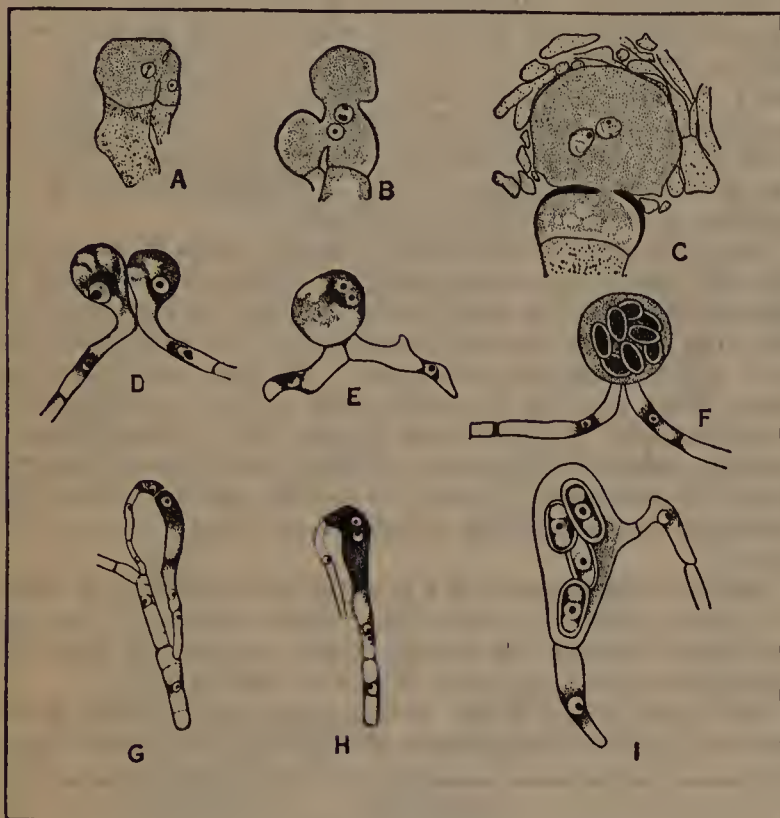
FIG. 6.—A, B. CONTACT AND GROWTH OF PROGAMETANGIA. C. DIVIDED PROGAMETANGIA FORMING GAMETANGIA AND SUSPENSORS. D. CONJUGATION. E, F, G. DEVELOPMENT OF ZYGOSPORE

ground stromata in which the reproductive organs are embedded. In *Endogone lactiflua* two sexual branches of unequal size—male and female—grow up side by side. They are multinucleate at first and from each a terminal cell containing a single nucleus is cut off. These cells unite together and from the larger, the female, there now arises an outgrowth which rapidly enlarges, and into this pass the two sexual nuclei. This outgrowth is the zygote, which not only develops a thick wall but becomes surrounded and embedded by a number of vegetative hyphae (fig. 7 a, b, c).



Its germination is unknown. *Endogone* has been included in the Ascomycetes and is of considerable interest as indicating a possible relation between that class and the Zygomycetes.

**Ascomycetes.**—The mycelium is composed of hyphae regularly segmented into portions containing one or several nuclei. Asexual reproduction is common and this class provides a rich variety of conidial fructifications. Many species may show several different



FROM (A) GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER), (B) GWYNNE-VAUGHAN AND BARNES, "THE FUNGI" (CAMBRIDGE UNIVERSITY PRESS), (C, D, E) LA REVUE GÉNÉRALE DE BOTANIQUE (E. ORLHAC, PARIS)

FIG. 7.—A. FORMATION OF COPULATION OPENING IN ENDOGONE LACTIFLUA. B. NUCLEAR MIGRATION. C. FORMATION OF HYPHAL SHEATH AROUND ZYGOTE. D—F. DEVELOPMENT OF ASCI IN EREMASCUS FERTILIS. G—I. DEVELOPMENT OF ASCI IN ENDOMYCES

types of reproduction on one and the same mycelium. There are many species in which the ascus fruit is rarely produced and there may consequently be many generations reproduced entirely by conidia. It is not, therefore, surprising to find a large assemblage of fungi (*Fungi imperfecti*) which are only known to reproduce asexually and many of which are believed to be incomplete forms of Ascomycetes.

The sexual reproduction of the lower ascomycetes (Protas-cineae) may be compared with that of certain Phycomycetes such as *Endogone*. In *Eremascus fertilis* the sexual branches arise from two neighbouring cells of a hypha and grow up side by side. They each receive a nucleus from their parent cells and then fuse together. The two nuclei unite and the zygote enlarges and forms a spherical ascus. The fusion nucleus divides and eight ascospores are formed (fig. 7 d, e, f). The main point in which *Eremascus* differs from *Endogone* is that the direct product of fertilization is in the latter a zygospore and in the former an ascus. This then is one of the essential differences that mark off the lower Ascomycetes from the Zygomycetes. The higher forms are distinguished by a further advance, in that the zygote instead of forming an ascus gives rise instead to one or many hyphae which eventually form a number of asci (ascogenous hyphae). Thus we have intercalated between the gametangium and the ascus a new mycelial generation—the diploid generation.

The development of this diploid generation is accompanied in many forms with a delay in the fusion of the sexual nuclei, so that the ascogenous hyphae contain paired nuclei (dikaryons). It is in the ascus that nuclear fusion is finally accomplished, to be succeeded immediately by the meiotic phase and the formation of spores.

The ascogenous hyphae, however, do not form an independent self-supporting mycelium. They are dependent on the haploid

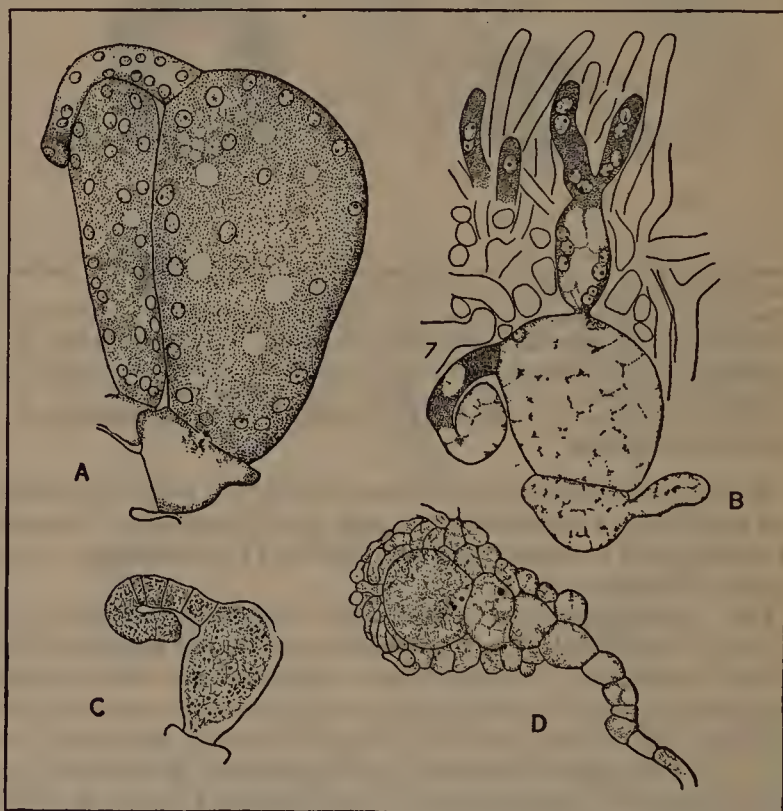
mycelium for their nutrition, and this is accomplished by the enclosure of the ascogenous hyphae in a simultaneous growth of vegetative hyphae from the parent mycelium. Thus we have formed the fruit body or ascophore, one of the characteristic structures of the higher ascomycetes, showing in the different families great variety in structure and organisation. Whilst in many families its development awaits the stimulus which originates in fertilization, in the higher forms it may reach an advanced stage of development before the sexual organs arise, buried in its tissues.

In *Eremascus* the two sexual organs are alike, but in the related *Endomyces* they are differentiated into a large female gametangium, the ascogonium and a smaller male, the antheridium (fig. 7, g, h, i). In the Euascomycetes this differentiation in sex is maintained and the ascogonium is usually characterised by the development of a receptive portion, the trichogyne. Both structures may be unsegmented, but in many families they may be divided by cross walls into several cells, the whole ascogonial branch (archicarp) thus consisting of a hypha of many cells, which is sometimes spirally coiled.

The antheridium shows no corresponding development, in fact it is possible to trace throughout the whole group the gradual dwindling in importance and final elimination of this organ.

With the cessation of the function of the antheridium and the establishment of some autogamic type of fertilization, the importance of the ascogonium itself begins to diminish. The functionless trichogyne disappears and finally the ascogonium itself is suppressed, and fertilization is effected between two undifferentiated cells of the haploid mycelium. These processes may be illustrated by reference to certain genera of the Pezizales.

In *Pyronema confluens* the large pear-shaped ascogonium bears



FROM (A, B) ZEITSCHRIFT FÜR BOTANIK (GUSTAV FISCHER), (C) "PROCEEDINGS OF THE ROYAL SOCIETY," (D) GWYNNE-VAUGHAN AND BARNES, "THE FUNGI" (CAMBRIDGE UNIVERSITY PRESS)

FIG. 8.—A, B. ASSOCIATION OF MALE AND FEMALE NUCLEI IN PYRONEMA CONFLUENS. C. FUSION OF ANTHERIDIUM AND SEPTATE TRICHOGYNE IN LACHNEA STERCOREA. D. ASCOGENOUS HYPHAE IN HUMARIA GRANULATA

at its upper end a tubular trichogyne, the tip of which fuses with the club-shaped antheridium. All these structures are multinucleate. The contents of the antheridium pass first into the trichogyne and then, by absorption of the intervening wall, into the ascogonium, where the male and female nuclei become associated (fig. 8 a, b). In *Lachnea stercorea*, though the antheridium is fused with the trichogyne, the latter is septate and no male nuclei pass from the antheridium into the trichogyne (fig. 8 c). In *Lachnea cretea* no antheridium is formed though the septate tri-



chogyne is still developed. In *Humaria granulata* the trichogyne has disappeared though the ascogonium has still the form of those described above and like them gives origin to the ascogenous hyphae (fig. 8 d). Finally in *Humaria rutilans* the ascogonium itself has disappeared and, with it, all trace of autogamous fertilization, which is replaced by the pseudogamous fusion of vegetative cells.

A parallel series can be traced in a related genus *Ascobolus* in which the ascogonium is many-celled. In *A. magnificus*, which is heterothallic, normal conjugation takes place between antheridium and trichogyne, in *A. furfuraceus* antheridia are absent. In one species *Ascobolus carbonarius* the antheridia are absent, but the long and often coiled trichogyne comes into contact with one of the oval, stalked conidia, borne on the mycelium, and fuses with it and thus, apparently, fertilization is effected.

This process finds an interesting parallel in one of the lichen fungi *Collema pulposum*. Here the archicarp, as in many lichen fungi, is a coiled thread terminating in a long slender trichogyne; the latter comes into contact with a conidium and fusion results. In other species of *Collema* the trichogynes, projecting above the surface of the thallus, get attached to their surface one or more uninucleate bodies, the so called spermatia, which are formed in flask-shaped bodies resembling pycnidia. As the name implies, these spermatia have been regarded as male sexual cells, but since they can be germinated in certain cases to form mycelia, it is possible that they are to be regarded as pycnospores their function as male cells being a secondary one.

It may perhaps be as well to point out, that these processes of modification and disappearance of the sexual organs, should not obscure the fact that the essential feature of fertilization is the fusion of two haploid nuclei, and it would appear that it is immaterial, whether these nuclei are derived from different sexual organs, antheridium and ascogonium, from the ascogonium alone, from an ascogonium and a vegetative cell, or from two vegetative cells. In every case the process which brings them together, whether fusion immediately results or not, marks the starting point of a new development, viz., the diploid generation, represented by the ascogenous hyphae. These hyphae eventually give rise to the asci and in the majority of the ascomycetes they are formed in a very characteristic way. As already stated the ultimate segments of these hyphae are binucleate and any one of them may grow out to a short branch, into which the two nuclei pass. This cell now curves over at the tip to form a hook, and the nuclei moving up to the summit divide there simultaneously. The spindles are so arranged that when the two cross walls are formed the summit of the crook contains two nuclei, whilst one is in the tip and another in the stalk (fig. 9).

In most cases the two nuclei at the summit fuse together and form the fusion nucleus of an ascus, which is formed by the further development of the parent cell. The point of the crook and the stalk lie close together and either of them may now become binucleate by the migration into it of the nucleus from the other. In this process the walls are perforated by the travelling nucleus. The binucleate cell so formed may now originate a new crook and so the process may be repeated several times.

The young ascus now enlarges, the nucleus also increasing in size, and finally the latter divides; this is followed by two further divisions and thus eight nuclei are formed, which become the centres in forming eight ascospores (fig. 10). The details of nuclear division in the ascus have been carefully studied in a number of forms, and there is no doubt that the first division in the ascus is the heterotype or reducing division (see CYTOLOGY). The two following divisions have, for the most part, the characters



FROM ZEITSCHRIFT FÜR BOTANIK (GUSTAV FISCHER)

FIG. 9.—A-F. PYRONEMA CONFLUENS: DEVELOPMENT OF ASCOGENOUS HYPHAE

of post meiotic divisions, but there is no general agreement as to their interpretation. In the account of the sexual process and development of the ascogenous hyphae already given, it has been assumed that the sexual nuclei are associated in pairs and pass as such (dikaryons) into the ascogenous hyphae; here the pairs may divide but later a pair of nuclei, by derivation male and female, fuse together in the ascus and so complete fertilization. In such a case the first division in the ascus is a reducing division and in the two succeeding divisions the haploid numbers of chromosomes will appear.

There are a number of forms however (*Sphaerotheca*, *Humaria*, *Lachnea*, *Ascobolus*) in which the nuclei in the ascogonium, however derived, have been described as fusing together. In this case, the nuclei in the ascogenous hyphae are diploid nuclei and the fusion in the ascus is a second fusion, and results in a nucleus with a fourfold number of chromosomes (tetraploid nucleus). Obviously a double process of reduction is necessary to restore the haploid nuclei of the sexual generation, and the second reduction is stated to take place during the second or third division. Further investigation is needed either to confirm or disprove the existence of double fusion and double reduction.

The weight of evidence on the whole favours the conclusion, that single fusion is the normal process in the Ascomycetes. In this respect they conform with the other large group of the higher fungi, the Basidiomycetes.

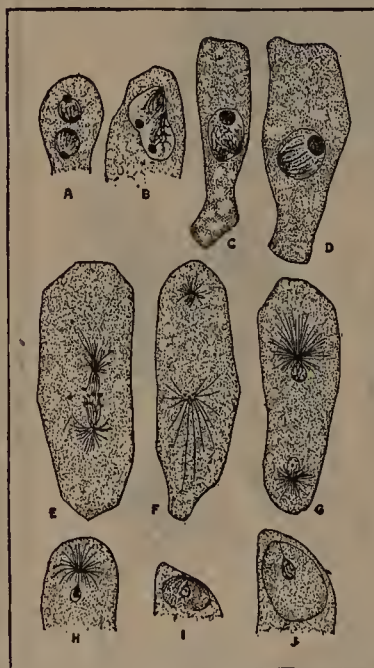
The mode of spore-formation in the ascus is peculiar. The eight nuclei formed in the third division show delicate radiations, extending from a centrosome, which meet around the nucleus and thus delimit a portion of the protoplasm on which a wall is secreted to form a young spore (fig. 10, h, i, j).

It has already been explained that, in the higher Ascomycetes, the developing ascogenous hyphae are enclosed by a development of the haploid mycelium, on which, in fact, they are parasitic. The whole structure which results is known as a fruit body or ascophore. In the simpler orders (Plectascales and Perisporiales)

the enclosure is complete, the sterile hyphae compacting together on the outside to form a completely closed investment. Such a fruit body is called a perithecium. In other orders (Hypocreales, Sphaeriales, Dothidiales) a perithecium is formed, which is often flask-shaped, and provided with a neck with a definite opening for the discharge of the spores (fig. 12).

The remaining orders have a fruit-body known as an apothecium. Here the numerous asci are assembled, together with sterile hyphae or paraphyses, in a continuous layer known as the hymenium (fig. 13). This is freely exposed on the surface of the ripe fruit body which may be a flat disc or a cup (Pezizaceae) or a convex, often stalked, structure (Helvellaceae).

The spores of many ascomycetes are explosively discharged from the asci; a process which is facilitated by their mucilaginous contents and the pressure of the



FROM E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER)

FIG. 10.—PHYLLACTINIA CORYLEA. A. YOUNG ASCUS WITH DICARYON. B-D. CAROLOGY. E-G. STEPS IN DIVISION OF PRIMARY ASCUS NUCLEUS (ERYSIPHE CICHORACEARUM). H-J. SPORE FORMATION

surrounding asci and paraphyses.

The Endomycetales are a small family in which (*Endomyces*, *Eremascus*) the asci result directly from the conjugation of the gametangia and are thus borne directly on the mycelium (fig. 7). The important family of the yeasts, Saccharomycetaceae, is included in this order. These are fungi which, living normally in liquid media, have the form of oval or spherical cells which reproduce by budding. Some forms, when grown under certain con-



ditions, can develop true hyphae and thus show their derivation from fungi of normal structure. Many genera have a sexual process represented by the conjugation of ordinary cells. The result is the formation of an ascus in which ascospores are formed (*Schizosaccharomyces*, *Zygosaccharomyces*). In *Saccharomycodes Ludwigii* the ascospores are formed in the ordinary yeast-cells and conjugation takes place between the germinating spores. The ordinary yeast cells so produced are thus diploid cells. The beer yeast (*Saccharomyces cerevisiae*) is generally regarded as parthenogenetic. (See YEASTS.)

The Exoascaceae is a family of parasitic fungi which grow on the higher plants, often producing malformation of the leaves, fruits, etc. The mycelium may develop in the deeper tissues, but eventually makes its way to the surface and the asci are produced between the epidermal cells, or more frequently they arise from hyphae which lie between the epidermis and the cuticle. The cells of the mycelium are binucleate, and in the young ascus the two nuclei fuse and then undergo division, eight spores resulting in the usual manner. In some species (*Taphrina*) the original spores may bud in the ascus and give rise to hundreds of small conidia.

When spores are sown in suitable culture fluids they bud after the manner of yeast cells and produce conidia. In two species of *Taphrina* it has been shown that these secondary conidia can conjugate in pairs by means of a short tubular process. The nucleus from one cell passes into the other and the binucleate cell so formed now puts out a germ-tube. Moreover, when the eight spores from one ascus are carefully isolated and germinated apart, it is found that they fall into two groups, the conidia of one group will not conjugate together but do so readily with any member of the other group. They are thus, like many of the Mucorini, heterothallic, and the separation into the two sexes must take place during the divisions in the ascus.

The Plectascales include the common saprophytic moulds *Aspergillus* and *Penicillium* of which some species—*Aspergillus*

e.g., hop mildew, American gooseberry mildew. They produce conidia in chains and numerous perithecia which bear characteristic appendages. The Perisporiaceae with a similar habit have dark coloured mycelium and are known as sooty moulds.

The three orders Hypocreales, Sphaeriales, Dothideales include families which have frequently been grouped together under the names of Pyrenomycetes. They have perithecia which, when mature, have a well-defined mouth (fig. 12). In some genera the



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 12.—PERITHECIUM OF *PODOSPORA FIMECEDA* IN LONGITUDINAL SECTION

fruit bodies are borne directly on the mycelium (*Sordaria*, *Chaetomium*) or isolated in the host tissues (*Venturia*) but more often they are borne on a stroma (*Nectria*, *Cucurbitaria*) or embedded in it (*Epichloe*, *Claviceps*, *Valsa*). The stroma may be flat or cushion-shaped, or immersed in the tissues of the host. In the more specialized forms the stroma may show a sterile basal stalk, the perithecia being limited to the upper part, where they may more efficiently distribute their spores (*Xylaria*). The Pyrenomycetes is by far the largest group of the Ascomycetes, a conservative estimate of the number of species being 10,000. Though the majority are saprophytes some well-known diseases of plants are caused by members of this group, e.g., canker in fruit trees (*Nectria*), ergot of cereals and other grasses (*Claviceps*), apple and pear scab (*Venturia*), most species of *Cordiceps* are parasites on insects.

The Pezizales include the forms with apothecia and they provide the largest and most elaborate fruit-bodies among the ascomycetes, e.g., *Morchella* which may be 10–12 inches in height.

In the Pezizaceae—the cup fungi—the apothecium is concave, saucer or cup-shaped, sometimes stalked. In the Geoglossaceae and Helvellaceae the ascophores are club-shaped or differentiated into a sterile stalk and fertile head, which may be folded or ridged in various ways to increase the area of the spore-bearing surface (fig. 13).

The Tuberales is a small group of fungi which include the well-known truffles (*Tuber* sp.). They live underground in the neighbourhood of trees and have been thought to be concerned in the formation of mycorrhizas. The hymenium lines internal chambers in the fruit-bodies.

The Laboulbeniales is an order of peculiar fungi, whose manifold structure has been made known by the investigations of Thaxter in America. They are minute plants from 1–10 m.m. in height which grow attached to the bodies of insects, especially beetles. They are dark brown in colour and consist of a basal receptacle which bears appendages, on which are the sexual organs. The female



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 13.—PEZIZA AURANTIACA (AFTER KROMBOLZ). NAT. SIZE

organ is essentially an ascogonium with a trichogyne and is fertilized by male cells or spermatia. The fertilized ascogonic cell (ascogonium) gives rise to a number of asci which are enclosed in a perithecial wall that develops around the female organ. Some species are probably heterothallic (*Amorphomyces*) but the male and female spores are associated together in the ascus, are shed and germinate together.

**The Basidiomycetes.**—The mycelium, like that of the Ascomycetes, is fully segmented, but in the haploid mycelium the segments are uninucleate. They differ from the Ascomycetes in the absence of sexual organs, whose functions are performed by

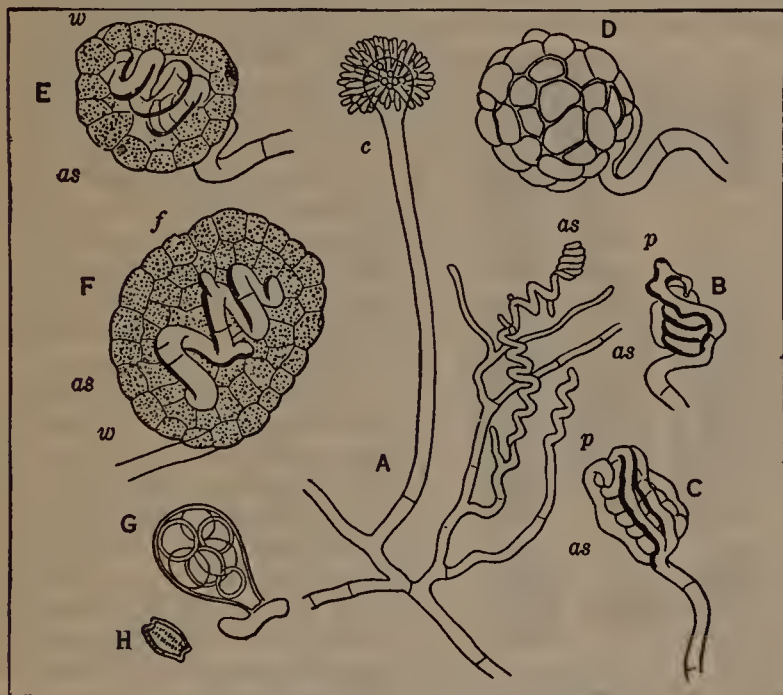


FIG. 11.—DEVELOPMENT OF *EUROTIIUM REPENS*

A. Small portion of mycelium with conidiophore (c) and young archicarp (as). B. Spiral archicarp (as) with the antheridium (p). C. The same, beginning to be surrounded by haphae forming perithecial wall. D. Perithecium. E, F. Sections of young perithecia: w. parietal cells, f. pseudo-parenchyma, as. ascogonium. G. An ascus. H. An ascospore

herbariorum, *Penicillium crustaceum* are the commonest and most ubiquitous of fungi. They reproduce themselves by a profuse production of conidia and also by closed (cleistocarpous) perithecia (fig. 11).

The Perisporiales are parasitic fungi living epiphytically, i.e., on the surface of their hosts, absorbing food materials by haustoria from the epidermal cells—or sending hyphae through the pores of the stomata into the interior of the host. The Erysiphaceae or mildews are the cause of disease in many cultivated plants,



pseudogamous vegetative fusions. The diploid mycelium which results is extensively developed, has a completely independent existence and in the higher forms, is, in fact, the only mycelium which can normally be distinguished.

Though sexual organs are absent the haploid mycelium is often sexually differentiated. Heterothallism occurs both in the Uredinales and Ustilaginales, and is widespread in the higher forms. In the latter, pseudogamous fusions presumably occur between



FROM (A, B, C, D) W. RUHLAND, "KENNTNISS DER INTERCELLUM KARYOGAMIE OEBER DEN BASIDIOMYCETES" (ARTHUR FELIX), (E, F) W. G. SMITH, "BRITISH BASIDIOMYCETES," (G) GWYNNE-VAUGHAN AND BARNES, "FUNGI" (CAMBRIDGE PRESS)

FIG. 14.—(A) *ARMILLARIA MELLEA*: YOUNG BASIDIUM WITH THE TWO PRIMARY NUCLEI, (B) AFTER FUSION OF THE TWO NUCLEI (*HYPHOLOMA APPENDICULATUM*), (C) BASIDIUM BEFORE THE FOUR NUCLEI, DERIVED FROM THE SECONDARY NUCLEUS OF THE BASIDIUM, HAVE PASSED INTO THE FOUR BASIDIOSPORES, (D) PASSAGE OF A NUCLEUS THROUGH THE STERIGMA INTO THE BASIDIOSPORE, (E) BASIDIUM AND SPORES (*AURICULARIA AURICULA-JUDAE*), (F) BASIDIUM AND SPORES, (*EXIDIA GLANDULOSA*), (G) *UROMYCES*

hyphae of the mycelia of different kinds, though in only a few cases have these actually been observed. Asexual reproduction by conidia and oidia occurs in both types of mycelia.

In the lower families the basidia are borne directly on the diploid mycelium, but in the vast majority of the forms they are borne on fruit bodies or sporophores. These are not formed, as in most Ascomycetes, as the immediate result of a sexual process (see above) but arise from the diploid mycelium at a time and stage in its development which are determined by physiological factors, such as nutritive conditions, humidity, light, etc. The basidium, like the ascus, is the gonotocont. In it the reduction of the chromosomes is effected but the daughter cells (usually four) resulting are exogenous, *i.e.*, borne on short stalks (sterigmata) outside the mother cell (fig. 14 d). Two kinds of basidium occur, those characteristic of the Autobasidiomycetes are, like the ascus, undivided (holobasidia). The Protobasidiomycetes have the basidia divided by septa into four cells (phragmobasidia) (fig. 14 e). The dividing walls may run transversely, *e.g.*, *Auricularia*, or longitudinally as in *Tremella* (fig. 14 f). The fertilization which takes place in the young basidium is followed immediately by the reducing divisions and the development of spores, but in the Uredinales and Ustilaginales, after the nuclear fusion, a resting stage, often very prolonged, may intervene. This may be accompanied by a thickening of the wall of the mother-cell, which may even become set free from the mycelium as a spore (teleutospore, chlamydospore). These "probasidia" as they may be called, can no longer behave as basidia and produce the spores; they conse-

quently "germinate," that is they produce a short vegetative outgrowth resembling a germ tube (promycelium), which functions as the basidium and bears the basidiospores (sporidia). Thus in these forms the probasidium is concerned with the distribution and perennation of the fungus as well as with the production of the basidiospores (fig. 14 g).

The basidiospores may be thin-walled and adapted for immediate germination, and this is the case of the Protobasidiomycetes and in some of the lower families of the Autobasidiomycetes. These thin-walled spores when germinated in water or nutrient solutions may sprout like yeast cells and produce gemmae or secondary conidia. In the higher families they are thick-walled and are resting spores. In the majority of Basidiomycetes the spores are discharged from the sterigmata, but only for a short distance (0.1–0.2 m.m.). They are, for the most part, distributed by air currents.

Sub Class. Protobasidiomycetes. The Auriculariales is an order of mostly parasitic forms of which the simpler representatives, *e.g.*, *Helicobasidium*, bear the basidia scattered on a loosely woven mycelium, but in the more typical forms, *e.g.*, *Auricularia*, the hyphae, which have gelatinous walls, are compacted to form fruit bodies, often of considerable size. The basidia are borne on the upper surface of these fruit bodies and are the terminal portions of hyphae which do not reach the surface, become somewhat wider and divide transversely into four cells. From each of these arises a long sterigma which projects above the surface of the thallus and develops a spore at its tip (fig. 14 e). The spores can germinate at once and bud off small curved conidia. The fruit body is formed throughout of binucleate cells; the origin of this



FIG. 15.—*PUCCINIA GRAMINIS*

A. Mass of teleutospores: t. on a leaf of couch-grass, e. epidermis ruptured, b. sub-epidermal fibres (after De Bary). B. Part of vertical section through leaf of *Berberis vulgaris*, with a. aecidium fruits, p. peridium, and sp. spermogonia (after Sachs). C. Mass of uredospores (ur), with one teleutospore (t); sh. sub-hymenial hyphae (after De Bary)

condition is unknown. The Jew's ear (*Auricularia auricula-Judae*) is a well-known representative of this order.

The Uredinales is a large order of parasitic fungi, known as the rusts, which are responsible for the diseases of many of the higher plants—ferns, conifers and flowering plants. Both kinds of mycelium, haploid and diploid are parasitic and may be found on the same host (autoecious) or on different hosts (heteroecious), sometimes belonging to widely different families. They are intercellular, highly specialised parasites, producing haustoria which penetrate the living cells of the host, and often stimulate the tis-

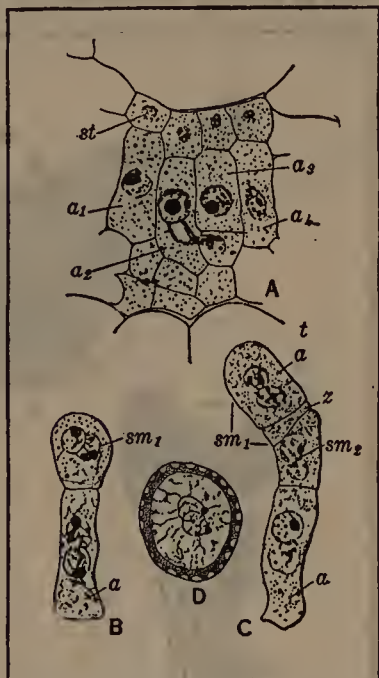


sues to increased growth and the formation of galls. They are often short-lived—attacking the leaves of the host and falling with them, but when they extend to the stems of perennial plants they are also perennial. No less than five kinds of spore may be produced in the life of one species, viz., aecidiospores, spermatia, uredospores, teleutospores and basidiospores (fig. 15). The aecidiospores and spermatia are borne on the haploid mycelium and appear early in the year. The first named are borne in fructifications known as aecidia, which are cup-shaped receptacles surrounded and enclosed by an investment (peridium, pseudoperidium), and containing rows of spores, which arise from a layer of cells at the base of the aecidium. The spores are binucleate and it has been shown that in the development of the aecidium, the basal cells are formed from uninucleate cells which, either become binucleate by the migration of a nucleus from a neighbouring cell, or, by uniting in pairs, give rise to a fusion cell with two nuclei (fig. 16). In either case we have a reduced sexual process by which the diploid generation is initiated, the first products of which are the aecidiospores. The spermatia are thin-walled cells of small size containing little protoplasm and a relatively large nucleus. They are borne in flask-shaped receptacles, the spermogonia. As the name indicates, they have been regarded as aberrant male sexual cells. This implies the previous existence of female sexual organs provided with some apparatus for the reception of spermatia. It has been shown that in certain forms, e.g., *Phragmidium violaceum*, the fertile cells when young cut off a terminal sterile cell (fig. 16) which may well represent the remains of a trichogyne, which in ancestral forms projected above the surface of the host. These

hypothetical ancestors would thus have a simple female sexual organ comparable with the archicarp of many Ascomycetes. The fact that all attempts to bring about infection of the host are by means of the spermatia lends strong support to the view that they are aberrant male cells. On the other hand there is evidence that in some species the haploid mycelia are heterothallic and that the conjugation of cells from two different mycelia are involved in the sexual act which precedes the formation of an aecidium. It is not without significance that spermogonia in these cases occur on *all* mycelia both (+) and (−). The spermatia are exuded from the spermogonia in drops of sweet fluid, which is sought by flies and other insects. Where drops of this liquid with the spermatia are transferred from the spermogonia on one mycelium to those on another sterile mycelium, the formation of aecidia is stated to follow immediately. Cytological details are unknown, but these observations, if confirmed and extended, may modify the conception now entertained of the morphological nature of the spermatia both in this and other groups in which they occur.

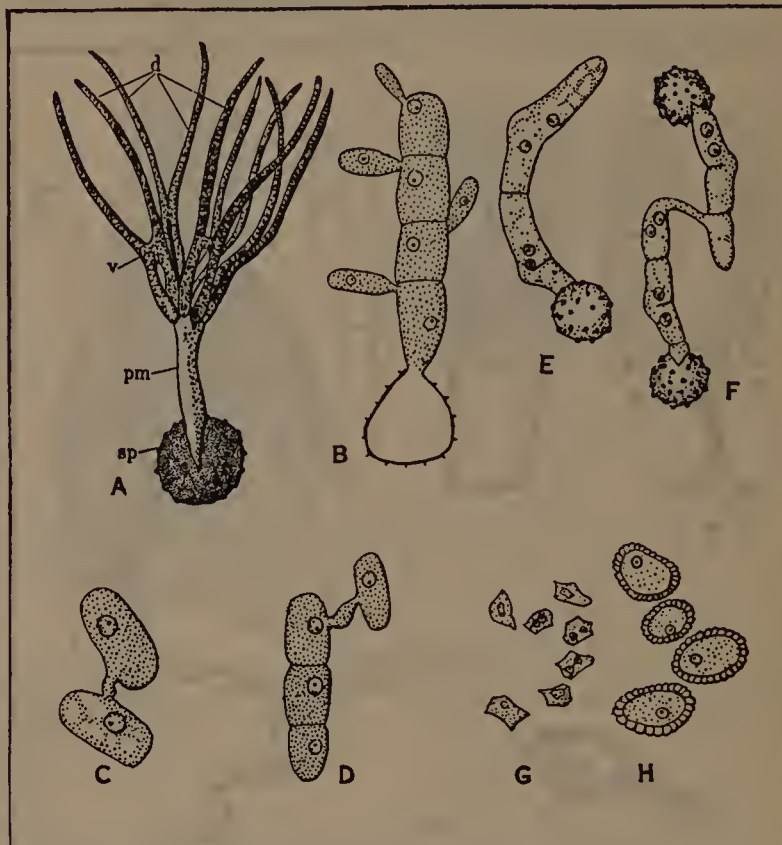
The aecidiospores germinate readily on the surface of the appropriate host and the germ tubes enter the tissues by way of the stomata. They give rise to a binucleate mycelium and on this in due course appear the uredospores. These are so-called "summer" spores, i.e., conidia of the diploid mycelium, and can infect fresh hosts and so spread the disease. Later in the year and on the same mycelium teleutospores are formed. These are typically thick-walled and resting spores. The uredospores are binucleate

and so are the young teleutospores, but in the latter the two nuclei fuse before their development is completed. The teleutospores are thus the probasidia. They germinate in due course and give rise to the promycelium—the basidium proper, on which after its division into four cells the four basidiospores, known as sporidia—are produced. These are uninucleate and can at once infect the proper host and develop the haploid mycelium. This



AFTER BLACKMAN IN STRASSBURGER, "LEHR-BUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 16.—*PHRAGMIDIUM VIOLACEUM*  
A. Portion of young aecidium: st. sterile cell, a. fertile cells; at  $a_2$  the passage of a nucleus from the adjoining cell is seen. B. Formation of the first spore-mother-cell (sm), from the basal cell (a) of one of the rows of spores. C. Further stage in which from sm, the first aecidiospore (a) and the intercalary cell (z) have arisen, sm<sub>2</sub>. Second spore-mother-cell. D. Ripe aecidiospore



FROM (B-H) E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER)  
(A) VINE, "STUDENT'S TEXT BOOK OF BOTANY" (ALLEN & UNWIN)

FIG. 17.—(A) GERMINATING RESTING-CONIDIA OF *TILLETIA CARIES*, (B) GERMINATION OF SMUT PORES (*USTILAGO SCABIOSAE*), (C, D) COPULATION OF SPROUT CELLS (*USTILAGO VIOLACEA*), (E, F) GERMINATING AND COPULATING PROMYCELIA (*CINTRACTIA MONTAGNEI*), (G) YOUNG BINUCLEATE SPORE FUNDAMENTS, (H) MATURE UNINUCLEATE SPORES (*USTILAGO HOLOSTEI*)

is the life history of one of the most complicated forms, the so-called eu-forms of which the black rust of wheat (*Puccinia graminis*) is an example. In this species the host of the haploid mycelium is the common barberry (fig. 15). In other species one or more of the spore types may be absent. The -opsis forms have no uredospores (*Gymnosporangium* sp.). In the brachy-forms the aecidia are absent but the spermogonia are accompanied by sori of uredospores, which in some cases arise as the result of a reduced fertilization, like that already described as taking place at the base of the aecidium. These primary uredospores thus appear to be homologous with aecidiospores. Other species have neither aecidia (or primary uredospores) nor spermogonia and are known as hemi-forms; there are micro-forms in which teleutospores alone occur. In the latter the binucleate condition is established at an early stage—probably by the migration of a nucleus from one cell to another of the haploid mycelium. The most reasonable interpretation of these forms with a shortened life history is that they have been derived from the more complete forms. The teleutospore is the spore form almost invariably present and the classification of the family is based largely on its structural peculiarities.

The Ustilaginales were regarded by Brefeld as showing a half-way stage in the evolution of the Basidiomycetes from the lower fungi and he placed them in a separate group, the Hemibasidiomycetes. The cytology of the group, however, leaves little doubt that they are true Basidiomycetes and form a parallel group to the Uredinales.

They are parasites on grain and fodder plants causing the well-known diseases smut and bunt. The mycelium, which is usually binucleate, often develops slowly at first and then grows



rapidly at a particular stage of development of the host and produces its spores, e.g., the smut of wheat (*Ustilago tritici*) attacks the wheat in the flower. The grains already infected are sown, the plant develops without external sign of disease and not until the ears are formed does the fungus develop in the flowers, and gives rise to a black powdery mass of spores. These chlamydospores are formed from binucleate hyphae which divide into short cells which separate, round themselves off and form the thick-walled chlamydospores. The two nuclei fuse in the spore which is, like the teleutospore of the host, uninucleate (fig. 17).

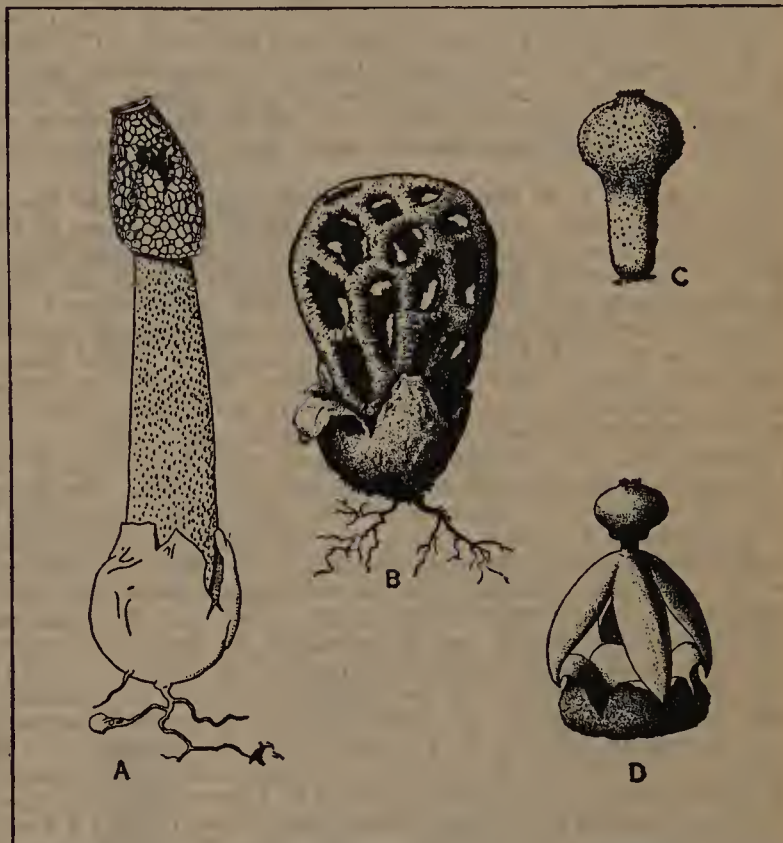
On germination the spores give rise to a promycelium. In the Ustilaginaceae the nucleus undergoes two successive divisions as in the Uredinales, and the promycelium (basidium) is divided by transverse walls into four cells. These may not form sporidia but may conjugate in pairs by clamp connections or short conjugating tubes (*Ustilago nuda*) (fig. 17), or they bud off small sporidia, which sprout like yeast cells and eventually conjugate in pairs (fig. 17). The binucleate cells, however formed, can sprout secondary cells or give rise to hyphae, either of which can infect a new host. In one species, *Ustilago Zeae*, the mycelium in the host is uninucleate and conjugation takes place at the appropriate time between cells of the hyphae, which then round off and form spores.

In the Tilletiaceae, the promycelium remains undivided, eight or more daughter nuclei are formed by division and a whorl of long curved sporidia arise at the tip of the promycelium. These fuse together in pairs, and from the fusion cell secondary sporidia may arise (fig. 17 a).

The Tremellales are a small family of saprophytic fungi with gelatinous fruit-bodies. Their mycelium is binucleate and gives rise to nearly spherical basidia. In these the fusion nucleus undergoes the usual divisions and the cell becomes divided by four vertical walls into four daughters from each of which a long sterigma grows up to the surface of the fruit body and develops a spore (fig. 14 f).

The general characters of the sub-class Autobasidiomycetes have already been outlined. Their basidia are undivided and they

broad cap or pileus. More advanced forms show the central stalk and cap-like pileus characteristic of the common mushroom and its relations the toad-stools. A further modification of the hymenium-bearing surface is the development of spines and wrinkles, folds, thin plates (gills) and of pits and tubes; all of which have the effect of increasing manifold the surface of the



FROM (A) W. G. SMITH, "BRITISH BASIDIOMYCETES" (B, C, D) E. GAUMANN, "VERGLEICHENDE MORPHOLOGIE DER PILZE" (GUSTAV FISCHER)

FIG. 19.—(A) MATURE PLANT SHOWING REMAINS OF VEIL (ITHYPHALLUS IMPUDICUS), (B) EXPANDED RECEPTACLE (CLATHRUS CANCELLATUS), (C) LYCOPERDON GEMMATUM, SHOWING EXTERIOR OF FRUCTIFICATION, (D) MATURE FRUCTIFICATION OF GEASTER CORONATUS

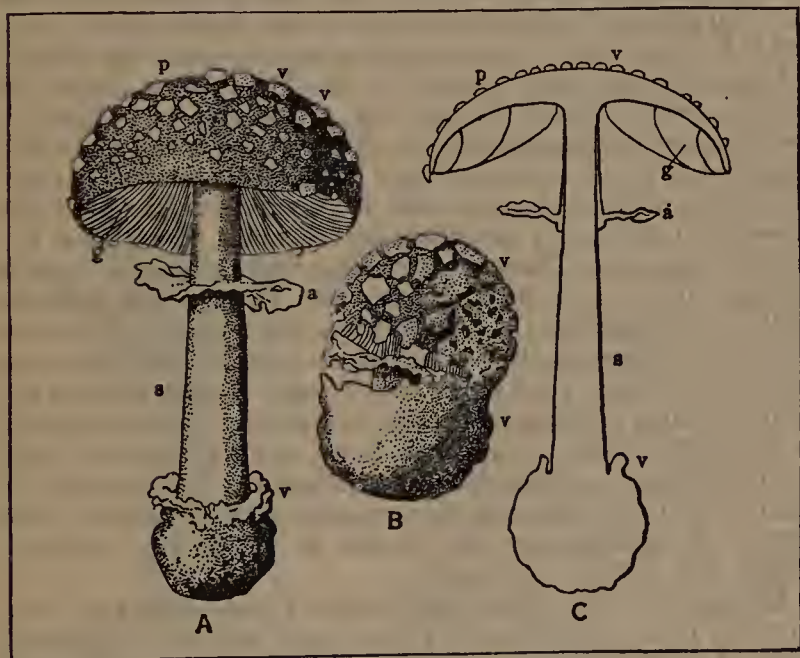


FIG. 18.—AMANITA MUSCARIA

A. The young plant. B. Mature plant. C. Longitudinal section of mature plant: p. the pileus, g. the gills, a. the annulus, or remnant or velum parziale, v. remains of volva, or velum universale, s. the stalk

are typically collected together in a continuous layer, the hymenium, in which are associated with them sterile hyphae or paraphyses. In the lower families the hymenium is borne on the surface of the fruit body. This may be a flat crust of indeterminate form and extent or, in species growing on vertical trunks of trees, may be bracket-shaped. In this case the hymenium is on the lower surface. A whole series of forms show that the bracket may narrow at its point of attachment and form a stalk and the fruit body is then differentiated into the stalk or stipe and the

hymenium, without correspondingly increasing the size of the sporophore (fig. 18).

In the higher families the fruit-body when young is a rounded spherical structure and the hymenial layers are differentiated from the inner tissues. In the Agaricales the fruit-body ruptures before the basidia are matured and so exposes the hymenium, but in the Gasteromycetes the opening of the fruit-body is delayed until the spores have been formed. In this last-named group the fungus fruit-body is often elaborately constructed and may be formed of fibrous tissue, gelatinous tissue, plectenchyma, etc. At maturity a rapid expansion of pseudo-parenchymatous tissue forming the so-called receptaculum may rupture the outer covering and expose the mass of spores, embedded in the mucilaginous remains of the fertile tissue, clinging to its surface (*Ithyphallus impudicus*, *Clathrus cancellatus*, fig. 19).

For further discussion of the symbiotic relations of Fungi with Algae see the article LICHENS; for the symbiotic relations of Fungi with the higher plants, especially orchids, heaths and forest trees, see the article MYCORRHIZA. For the rôle of the parasitic Fungi in plant diseases see PLANTS, *Plant Pathology*. See also DRY ROT; MUSHROOM; PUFFBALL; SMUT AND BUNT; TRUFFLE; YEAST AND FERMENTATION.

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**ACAULESCENT**, a term used of a plant apparently stemless, as dandelion, the stem being almost suppressed.

**ALBURNUM** (sapwood), the outermost and youngest part of the wood of a tree, through which the upward water current mainly passes. It is distinguished from the harder inner and older wood, the duramen or heart-wood.

**ANATOMY OF PLANTS**: see the section *Anatomy* under

PLANTS; also in the same article the ensuing sections on *Vascular System*, *Cambium* and *Cytology*. See further the separate articles on ROOT and SEED and various sections under the articles FLOWER; LEAF; STEM.

**ASCUS**, a botanical term for the membranous sacs containing the reproductive spores of fungi (*q.v.*) belonging to the group *Ascomycetes* (Gr. ἀσχος, a bag). Various compounds of the word are used, *e.g.*, *ascophorous*, producing *asci*; *ascospore*, spore developed in the ascus; *ascogonium*, organ producing it, etc.

**AUTOGAMY** (from Gr. αὐτός, self, and γαμία, marriage), a botanical term for self-pollination. (See ANGIOSPERMS.)

**AUXANOMETER** (Gr. αὐξάνειν, to increase, μέτρον, measure), an apparatus for measuring rate of growth of plants.

**AXILE** or **AXIAL** (related to the axis), used technically in botany. An axile placentation is one in which the ovules are attached to the axis.

**BUD**: see FLOWER; LEAF.

**BULB**, the name applied to the structure formed by many plants from a bud, the outer leaves of which are thick and fleshy by reason of the reserve food-products with which they are crowded. This enables the plant to tide over an unfavourable period, such as a cold or dry spell, safely buried in the earth, and to be ready to come into flower as soon as good conditions return. Bulbs are very characteristic of arid regions such as the South African Karroo. Many of the best-known spring flowers are bulbous, *e.g.*, the daffodil, narcissus, hyacinth, etc. The crocus is not technically a bulb, the structure often referred to as such in this plant being a corm, which is the thickened base of a stem.

**BUR** or **BURR**, a prickly fruit or head of fruits, as of the burdock. Also a woody outgrowth on the trunk of a tree, the effect of a crowded bud-development.

**CADUCOUS**, a botanical term for "falling early," applied, *e.g.*, to the sepals of a poppy which fall before the petals expand.

**CAESPITOSE**, a botanical term for "growing in tufts," like many grasses.

**CHLOROSIS**, the botanical term for loss of colour in a plant-origin, a sign of disease.

**GYMNOSPERMS**. All living seed-bearing plants are divided into two groups, the Gymnosperms and the Angiosperms (*q.v.*), and it is certain that these two groups are only distantly related, if indeed they are directly related at all. The primary distinction between the two lies in the fact that, at the time of pollination, the ovule (or rudimentary seed) is freely exposed, and the pollen deposited on it (or very rarely near it) in Gymnosperms (indicating plants with naked seeds), but in Angiosperms is wholly enclosed in an ovary, on a specialized part of which (the stigma) the pollen is deposited. There are other important differences, both in anatomy and in reproductive structures. In particular the prothallus (or embryo-sac) is a much larger and more massive structure in Gymnosperms than in Angiosperms, and (with the exception of two tropical genera) the female organ characteristic of the group is a large archegonium similar in structure and development to the much smaller archegonium found in all mosses and ferns and their allies, but of which no trace is found in Angiosperms. As regards anatomical features no companion cells are found in the phloem of Gymnosperms, nor, except in one division, are true vessels met with in the wood.

Although no other living plants besides Gymnosperms and true flowering plants (Angiosperms) have seeds, yet fossil representatives of the club mosses are known which possess such structures. These plants are, however, so clearly and definitely related to the club mosses (Lycopodiaceae) on other grounds, and not to the Gymnosperms, that it is not necessary to discuss them further. (See PTERIDOPHYTES and PALAEOBOTANY: *Palaeozoic*.)

The Gymnosperms are of special interest on account of their great antiquity, which far exceeds that of the true flowering plants, and as comprising different types which carry us back to the Palaeozoic era and to the forests of the coal period. It is not surprising in a group of such antiquity to find that some divisions are wholly extinct. There are, in all, seven of these divisions of which three are extinct, one is represented by a single living species, the maidenhair tree, common enough in cultivation but



almost extinct in the wild state, and three are flourishing living divisions, though only one of these, the Coniferales (pines, cedars, larches, firs, yews, etc.) is a really large and important division of existing plants.

The seven divisions of the Gymnosperms show many indications of fairly close relationship and this appears to indicate that the whole group had a common origin, though this view is not by any means certain and is not universally accepted. If we accept the view that all the Gymnosperms had a common origin then there can scarcely be any doubt that the group from which they were evolved was the Filicales or true ferns, the resemblance between the latter and the most primitive division of Gymnosperms, the Pteridospermae or Cycadofilicales, being very striking. (See PALAEOBOTANY: *Palaeozoic*.)

Although the reproductive structures of the Gymnosperms are often described as "flowers," it seems better to avoid this term, as implying a resemblance, which scarcely exists, to the "flowers" of Angiosperms. The term "cone" will, therefore, be used throughout this article in preference to "flower," except in the case of the highest division, the Gnetales, where the resemblance to Angiosperms is more obvious.

The seven divisions of Gymnosperms are as follows:—

I. PTERIDOSPERMAE or CYCADOFILICALES. Wholly extinct. (See PALAEOBOTANY: *Palaeozoic*.)

II. CYCADALES. A living division, also represented in the Mesozoic.

III. BENNETTITALES. Wholly extinct. (See PALAEOBOTANY: *Mesozoic*.)

IV. GINKGOALES. Mostly extinct, with a single living species.

V. CORDAITALES. Wholly extinct. (See PALAEOBOTANY: *Palaeozoic*.)

VI. CONIFERALES. By far the largest and most important division of living Gymnosperms.

VII. GNETALES. Includes only three genera, with no known fossil representatives, but with some characters very suggestive of Angiosperms.

No further reference will be made here to the extinct divisions of Gymnosperms.

The living Gymnosperms agree in the following characters: Woody plants. Cones unisexual, monoecious or dioecious. Perianth not present except in Gnetales. Ovules naked, usually borne on leaf-like structures. The single megaspore enclosed in the nucellus becomes filled with tissue (prothallus) before fertilization (partially only or not at all in *Gnetum*); the microspore develops at least four nuclei (usually four to six) of which two are the male cells, very large and actively motile in Cycads and *Ginkgo*, much smaller and only motile in so far as they are passively carried by the pollen tube, in Coniferales and Gnetales.

Some account will now be given in turn of each of the four living divisions.

#### CYCADALES

**General.**—This division includes nine genera and over 80 species. It consists of plants with



FROM LOTSY, "VORTRÄGE ÜBER BOTANISCHE STAMMESGESCHICHTE" (FISCHER)  
FIG. 1.—ENCEPHALARTOS GHEL-LINCKII

tuberous or columnar stems, seldom branched, often clothed with an armour of petiole bases as in the stems of ferns, and terminating in a crown of large pinnate leaves (bi-pinnate in one genus). The plants are dioecious, with the cones always compact, with numerous sporophylls spirally arranged on an axis, except in female plants of *Cycas*, which bear on the main stem a loose rosette of leaf-like sporophylls each bearing from 2 to 6 or 8 ovules.

The cycads are practically confined to tropical and subtropical regions and are fairly equally divided both between northern and

southern and between eastern and western hemispheres. *Zamia* includes over 30 species which extend from Southern Florida to Chili. *Cycas* has only about 16 species, but they range from Japan to Australia. *Macrozamia* with 14 species is confined to Australia, while *Encephalartos* with 12 species is wholly South African. No other genus has more than three species. *Dioon* and *Ceratozamia* are both restricted to South Mexico, and *Bowenia* to Australia,



FIG. 2.—BOWENIA SPECTABILIS  
FROND

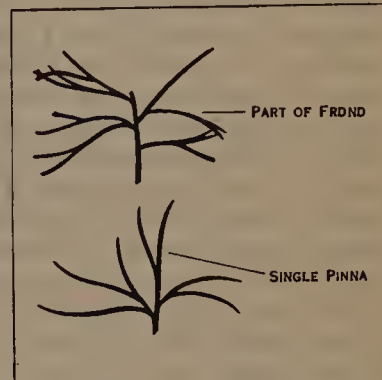


FIG. 3.—MACROZAMIA HETEROMERA  
SINGLE PINNA

while *Microcycas* and *Stangeria* occur only in West Cuba and South Africa respectively.

Externally some of the larger cycads closely resemble palms, others having an equally close resemblance to tree ferns, while so closely do the smaller species approximate to ferns in appearance (when not in cone) that *Stangeria* was actually first described (by Kunze in 1835) as a species of the fern *Lomaria*.

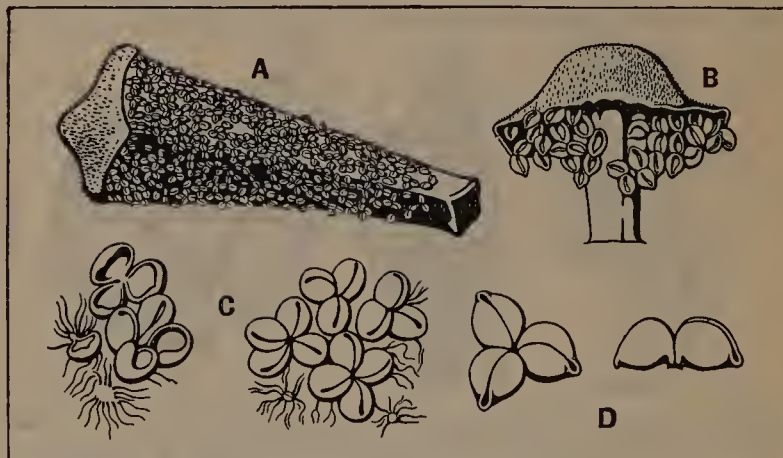
Cycads are characteristically very long lived and slow growing and certainly reach an age of upwards of a thousand years, probably much more.

The armour of dead leaf bases found on the old stem (fig. 1) is more particularly characteristic of the columnar forms, and is not found in *Bowenia* and *Stangeria*.

In the tuberous forms the stem is usually more or less subterranean, but may be very massive, like a gigantic carrot. The leaves of *Cycas* consist of a long rachis bearing numerous linear leaflets, each with a single midrib and no other veins. When young these leaflets are coiled up like the leaves of a fern. In most other cycads the leaves are similar except that the leaflets contain a number of parallel veins, e.g.



FIG. 4.—ZAMIA OTTONIS  
MALE CONE



AFTER ENGLER AND PRANTL, "DIE NATÜRLICHEN PFLANZENFAMILIEN" (ENGELMANN)  
FIG. 5.—MICROSPOROPHYLLS OF CYCADS. A. CYCAS CIRCINALIS. B. ZAMIA INTEGRIFOLIA. C. PARTS OF A. D. PARTS OF B

*Dioon* and *Encephalartos*. *Stangeria* has only a few leaflets on the rachis and each is traversed by a midrib from which simple or forked veins pass off at a wide angle. The leaves of *Bowenia* differ from those of other genera in being bi-pinnate (fig. 2). It is only in *Cycas* that the young leaflets are conspicuously coiled, the remaining genera showing little or no trace of this character. In *Macrozamia heteromera* the narrow pinnae are dichotomously branched almost to the base (fig. 3). In some forms, such as most of the species of *Encephalartos*, the margins of the leaflets are



spinous. In *Ceratozamia* the broad petiole base is characterized by the presence of two lateral spinous processes suggestive of stipules, and comparable with the stipules of Marattiaceous ferns.

**Cones.**—The “male” (or microsporangiate) cones of cycads (fig. 4) are very uniform in structure, and from one to a hundred may be produced in one season. Each consists of an axis bearing crowded, spirally disposed sporophylls, which are often wedge-shaped and angular, while in other cases they consist of a short, thick stalk terminating in a peltate expansion or prolonged upwards in the form of a triangular lamina (fig. 5). The crowded sporangia (pollen-sacs) are found on the lower side of the sporophyll and are often arranged in more or less definite groups (or “sori”). The sporangia break open when ripe by a slit radiating from the centre of the sorus. The sporangia are large, not unlike those of *Angiopteris* (a Marattiaceous fern) and their walls are several layers of cells in thickness. Each sporangium contains several oval spores which develop into pollen grains before they are set free. In this process each spore cuts off a small but persistent “prothallial cell,” and immediately divides again to cut off an almost equally small “generative cell,” the remaining nucleus, occupying the larger part of the spore cavity, being the “tube nucleus.” In this 3-celled condition the pollen is shed.

The female plants bear cones which in most genera occur singly in the centre of the crown, but in *Encephalartos*, *Bowenia* and *Macrozamia* from two to several may be found. In some cases these female cones reach an enormous size, that of *Encephalartos Caffer* being up to a yard in length and weighing as much as 100 lb., while that of *Macrozamia Denisoni* may be as long, though its weight seldom exceeds 60 lb. The smallest cones are those of *Zamia*, that of *Zamia pygmaea* being sometimes less than 3 cm. in length. The sporophylls usually have some, often a close, resemblance to those of the male cone, and are clearly homologous with them.

The most primitive type is evidently *Cycas*, in which the sporophylls are arranged round the apex like a crown of foliage leaves and are definitely leaf-like in form. In *C. revoluta* and *C. circinalis* each may produce several laterally attached ovules, but in *C. Normanbyana* the sporophylls are shorter and the ovules are reduced to two. In all other genera the cone is a much more definite and compact structure, but the sporophylls of *Dioon* and *Stangeria* terminate in a leaf-like up-turned process, and are clearly comparable with those of *Cycas*. In some of the remaining genera the sporophylls are shorter with thick peltate heads, and each bears two ovules on the lower surface (fig. 6). The young ovule consists of a spherical or ovoid rather massive nucellus, sur-

into it by the evaporation of a drop of liquid which oozes out from the micropyle at the time of pollination, as in conifers) and the tip of the pollen chamber, as well as the micropyle, closes and hardens, thus completely enclosing the pollen grains, of which from half a dozen to a dozen are usually found here. Later these develop pollen tubes as described below.

While these changes are going on, a large cell, the megaspore, makes its appearance in the central region of the nucellus, rapidly

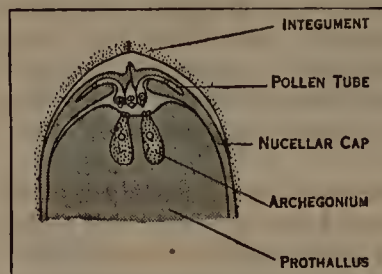


FIG. 7.—SEMI-DIAGRAMMATIC LONGITUDINAL SECTION OF A PART OF CYCAD OVULE BEFORE FERTILIZATION

increases in size, and ultimately absorbs the greater part of the nucellus. Its nucleus divides repeatedly and cells are produced from the peripheral region inwards, which eventually fill the spore cavity with a homogeneous tissue, the prothallus. From one to ten separate superficial cells at the apex of the prothallus now increase in size. Each cuts off a small cell at the top, which divides to form the small two-celled neck of the archegonium, the lower cell enlarging rapidly and becoming the egg-cell, its nucleus cutting off another small nucleus (which soon disappears) just before fertilization (fig. 7). In *Microcycas* a very large number of archegonia (up to 200 exceptionally) are produced all over the prothallus.

During the development of the prothallus the pollen chamber has enlarged both downwards and outwards, and eventually forms a fairly large chamber open below to the archegonia, which themselves lie at the bottom of a shallow depression in the apex of the prothallus, the “archegonial chamber.” Each pollen grain at once begins to put out a tube which grows laterally into the nucellus just below its outer surface. The apical part of the nucellus is almost the only part remaining by this time, and is known as the “nucellar cap.” Close inspection of the outer surface of the nucellar cap reveals several dark lines radiating from the beak outwards for about 2 mm. and these mark the positions of the pollen tubes. The “tube nucleus” of the pollen grain passes into, and remains in, the pollen tube, while the pollen grain hangs suspended by its tube in the pollen chamber (fig. 7). The “generative cell” divides to form another small sterile cell, the “stalk cell” and a much larger cell the “body cell,” which continues to enlarge (as does that part of the tube to which the grain is attached) and finally divides once more into two equal hemispherical cells, in each of which a single very large and actively motile spermatozoid is produced (fig. 8). (In *Microcycas* 8 to 10 body cells and 16 to 20 sperms are formed in each pollen tube.) In the course of the last division two small bodies known as “blepharoplasts” make their appearance just outside the nucleus, and after division is complete one of them remains in each spermatozoid where it

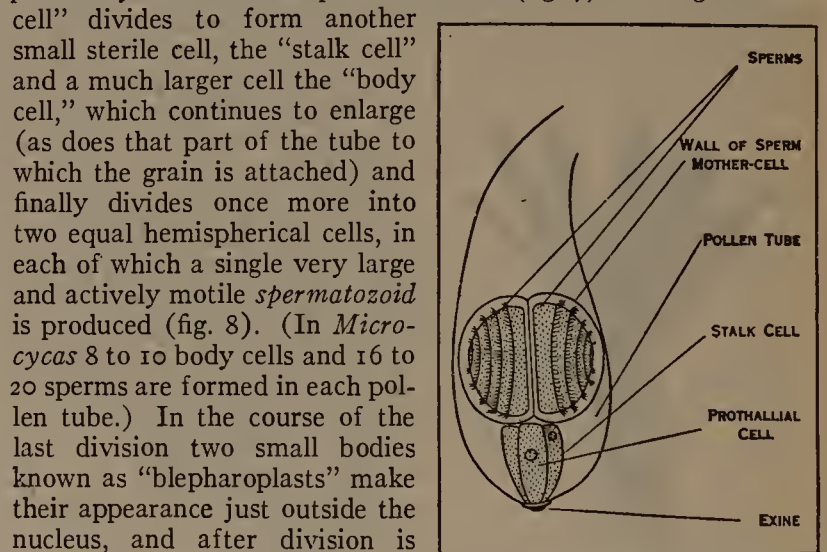
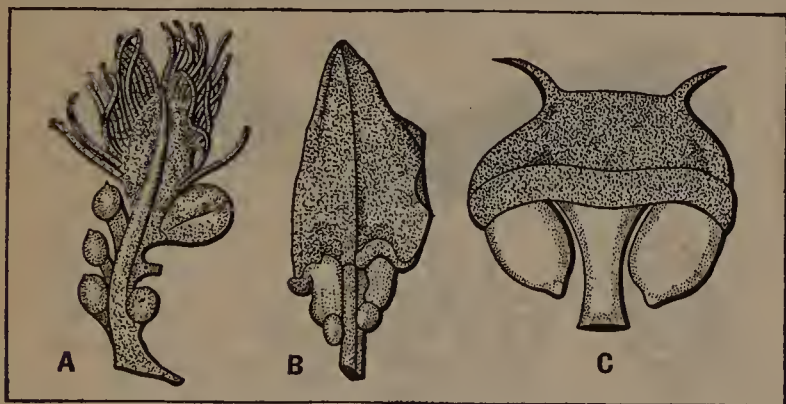


FIG. 8.—CYCAD POLLEN TUBE WITH SPERMS IN MOTHER CELLS

gradually gives rise to a spiral band which passes round and round the outside of each sperm while from the outside of the band innumerable fine hair-like cilia are produced which, by their active movements, enable the sperms to swim about, first in the two cells within which they are formed, then in the part of the pollen tube adjacent to the grain after the cell walls break down, and finally in the film of moisture covering the archegonial chamber, after the bursting of the pollen tube. At last one penetrates the neck cells of an archegonium and so finds its way into the egg cell, where the sperm nucleus slips from its ciliated sheath of protoplasm and swiftly passes down to fuse with the large egg nucleus.



FROM LOTS, "VORTRÄGE ÜBER BOTANISCHE STAMMESGESCHICHTE" (FISCHER)

FIG. 6.—MEGASPOROPHYLLS OF CYCADS: A. CYCAS; B. DION; C. CERATOZAMIA

rounded by the integument. The small round opening at the apex of the integument is known as the micropyle.

**Fertilization and Development.**—The pollen is carried by the wind, or very rarely, perhaps, by small beetles or other insects, to the micropyle and lodges there. Meanwhile the tip of the nucellus projects into the base of the micropyle in the form of a tiny beak, at the exact tip of which a fine hole appears, becoming somewhat wider below. This narrow but relatively deep hole, the “pollen chamber,” being exactly below the centre of the micropyle, the pollen grains pass into it (or, in some cases at least, are drawn



It is noteworthy that cycad sperms are the largest known in either plants or animals, and the only ones big enough to be definitely seen under ordinary lighting conditions, and while still living, with the naked eye, the largest of them reaching a diameter of more than a quarter of a millimetre. It is no less remarkable that sperms had been observed repeatedly in every other great group of both plants and animals (excepting *Ginkgo*) many years before they were ever seen in cycads, although the discovery of motile sperms in Gymnosperms had been predicted nearly 50 years earlier by the great German botanist Hofmeister. They were actually seen for the first time in *Cycas* in 1896 by a Japanese botanist, S. Ikeno, and shortly afterwards in *Zamia* by H. J. Weber, and since that time they have been carefully studied in most of the other genera.

Following fertilization, the fusion nucleus divides repeatedly till from 250 to about 1,000 nuclei are scattered through the protoplasm of the archegonium. These nuclei tend to be more closely aggregated at the base, and cell walls first appear in this region, thus forming a tissue at the base of each fertilized archegonium. An ephemeral tissue may also form throughout the archegonium, as happens in most genera, subsequently breaking down to form a cavity, or the centre of the archegonium may become a large vacuole at an earlier stage, as in *Cycas*. In either case the structure thus formed constitutes the proembryo. A compact group of cells at the extreme base forms the actual embryo, and the cells immediately above these elongate very much and eventually form a very long coiled and tangled suspensor which carries the embryo deep into the prothallus where it grows to about three-quarters of the length of the latter and absorbs about one-quarter of its tissue.

The mature embryo consists of an axis (the hypocotyl) terminated, at the end next to the suspensor, by a rudimentary root (the radicle) enclosed in a hard covering, the coleorhiza, and bearing at the other end a pair of large seed leaves or *cotyledons*, often fused together at their tips, and enclosing between them a minute terminal bud, the plumule. The integument of the ovule has now become the *testa* of the seed and is differentiated into three layers, an outer, thick, fleshy and brightly coloured one, in the inner part of which several vascular strands run up from the base, a thin hard woody layer, and a very thin inner fleshy layer containing a second set of vascular strands.

**Anatomy.**—The anatomy of the cycads presents many features of interest. Only a brief reference to one or two of the most striking of these is possible here. The wood is rather soft and laxly arranged and occupies a relatively small part of the thickness of the stem, though the vascular cylinder very slowly increases in thickness in the same manner as in woody Dicotyledons. Sometimes, as in *Cycas*, there is a double ring of vascular strands. In connection with the leaves two strands often branch off from the central cylinder on the opposite side to a leaf, pass spirally round in the cortex in opposed directions and pass into the petiole of that leaf, where they break up into a larger number of strands. This arrangement of leaf trace strands is peculiar to cycads, and the strands themselves are often known as girdles. For further anatomical details reference may be made to *The Living Cycads* by C. J. Chamberlain.

**Classification.**—Something has already been said about the characteristic features of certain genera. It will, however, be convenient to conclude with a key to all the genera, and the usual classification of the Cycadales, as follows:—

Division CYCADALES. Only family Cycadaceae.

Tribe A. Female plant with separate leaf-like sporophylls on the main stem. Leaflet with a midrib only. Cycadeae. *Cycas*.

Tribe B. Sporophylls always in compact cones. Zamieae.

Sub-tribe I. Leaflet with midrib and lateral veins. Stangerieae.

*Stangeria*.

Sub-tribe II. Leaflet with several parallel veins. Euzamieae.

a. Leaves bi-pinnate. *Bowenia*.

b. Leaves simply pinnate.

(i.) Megasporophylls (Carpels) with a terminal leafy part.

\*Ovules on a cushion-like placenta. *Dioon*.

\*\*Ovules sessile. *Encephalartos*.

(ii.) Megasporophylls peltate.

\*Sporophyll terminating in two horns. *Ceratozamia*.

\*\*Sporophyll with a spinous projection in the centre. Leaflets usually forked. *Macrozamia*.

\*\*\*Megasporophyll flat outside.

†Microsporophyll not peltate. *Microcycas*.

††Microsporophyll peltate like the carpel (fig. 4). *Zamia*.

Recently some very interesting hybrids have been obtained by



FROM ENGLER AND PRANTL, "DIE NATÜRLICHEN PFLANZENFAMILIEN" (ENGELMANN)

FIG. 9.—GINKGO LEAF SHOWING VEINS

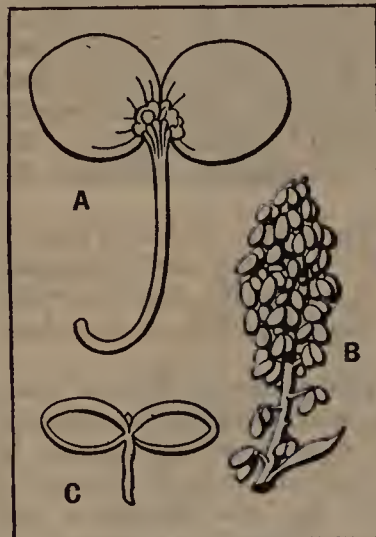
crossing various species of *Zamia* with others of the same genus and with species of *Encephalartos* and *Macrozamia*.

#### GINKGOALES

*Ginkgo biloba*, the maidenhair tree, is the solitary survivor of this ancient stock. As already mentioned it is almost extinct, but a few presumably wild trees have been recorded by travellers in parts of China. It is commonly cultivated in gardens of the far east, and is often also grown in North America and Europe and elsewhere. The trees are dioecious and may reach a height of 30 metres; they are freely branched and of pyramidal shape, with a smooth grey bark. The leaves (fig. 9) have a long slender petiole terminating in a fan-shaped lamina which may be entire or two-lobed or subdivided into several narrow segments. The veining is very characteristic and like that of many ferns, e.g., *Adiantum*; the lowest vein in each half of the lamina follows a course parallel

to the edge, and gives off numerous branches, which usually fork as they spread in a palmate manner towards the leaf margin. The foliage leaves occur either scattered on long shoots of unlimited growth or crowded at the apex of short shoots (spurs), some of which may subsequently elongate into long shoots.

The "cones," which are very unlike those of cycads and much reduced in comparison, are borne, usually several together, on spur shoots, in the axils of scale leaves. The "male" cone consists of a stalked central axis bearing a number of loosely disposed sporophylls. Each of these is formed of a slender stalk terminating in a small knob, from the inner side of which two



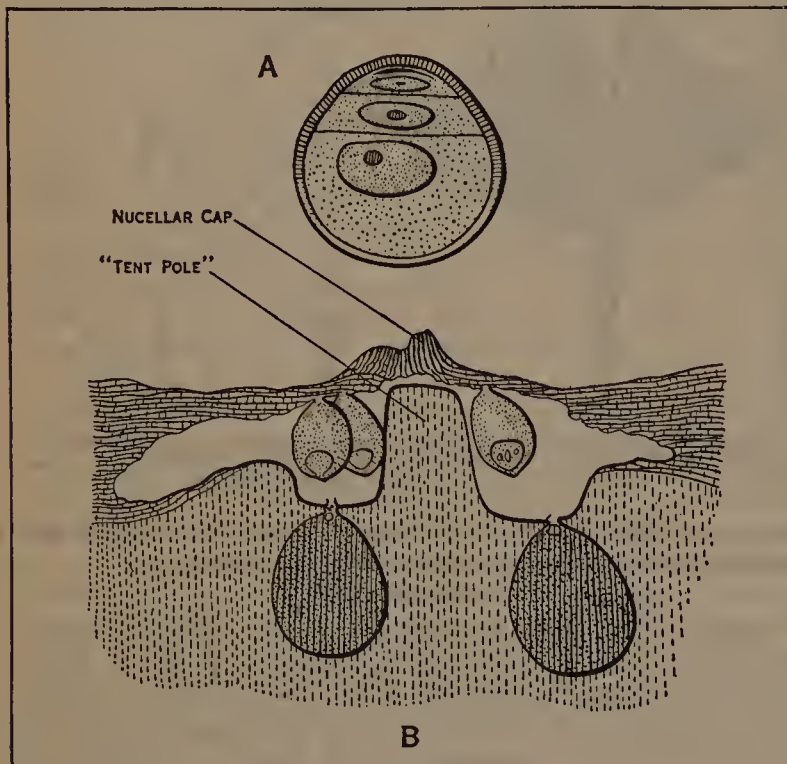
"ANNALS OF BOTANY," SEWARD AND GOWAN

FIG. 10.—GINKGO BILOBA: A. FEMALE CONE; B. MALE CONE; C. SINGLE MICROSPOROPHYLL

(rarely three or four) ovoid sporangia hang obliquely (fig. 10). Each sporangium opens by a longitudinal slit, as in cycads (fig. 10). The first cell cut off by the microspore is a small and ephemeral prothallial cell. Subsequently all the same cells are produced as in cycads (fig. 11), and in the same order, but besides the extra prothallial cell there are some minor differences in the later development, e.g., the pollen tube is freely branched, the tube nucleus eventually passes back into the grain, which it does not do in cycads, and the two sperms are somewhat smaller than those of cycads, though their shape and structure are precisely the same.



The "female cone" has the form of a long naked peduncle, bearing a single ovule on either side of the apex (fig. 10), the base of each being enclosed by a small saucer-shaped structure, the collar, which probably represents a sporophyll. The young ovule is very similar to that of cycads, a large pollen chamber occupying the apex of the nucellus. The early development of the prothallus takes place as in cycads, but eventually a short thick vertical col-



FROM HIRASE, "FÉCONDATION ET EMBRYOGÉNIE DE GINKGO BILOBA"

FIG. 11.—GINKGO BILOBA. A. RIPE POLLEN GRAIN. B. SECTION OF PROTHALLUS AND NUCELLAR CAP AFTER POLLINATION

umn grows up from the centre and supports the remains of the nucellar cap, which develops much in the same manner as in cycads (fig. 11). There are usually only two archegonia. The sperms were first observed in 1898 by a Japanese botanist, S. Hirase. The proembryo is similar to that of cycads, and the general organization of the embryo and its relation to the seed are almost identical except that no suspensor is formed. The ripe seed is brownish yellow in colour, about the size of a small plum, and with the same layers in the testa as in cycads. The middle woody layer has usually two (sometimes three) longitudinal ridges. The seed falls soon after (rarely before) fertilization and before the embryo is fully developed.

The anatomical structure of *Ginkgo* is very similar to that of conifers, and the presence of a few large and much elongated secretory sacs in the pith of the stem is a specific character, while the two leaf traces passing direct into the petiole are also characteristic.

In its more obvious characters *Ginkgo* agrees with the conifers, and before the discovery of the motile sperms it was generally regarded as one. But in most of its more recondite characters it shows a very marked similarity to the cycads and may perhaps be more nearly related to them than to any other division of the Gymnosperms. In any case it is clearly intermediate in the sum of its characters between the cycads and the conifers, as well as showing distinct evidence of relationship with the fossil division Cordaitales, and is one of the links in the chain of evidence which goes to support the view that all the Gymnosperms had a common origin and a Filicinean ancestry.

#### CONIFERALES

**General.**—The plants included in this, the largest and most important, division of Gymnosperms are a less homogeneous assemblage of forms than the cycads, and include approximately 46 genera with about 470 species. While the cycads are all included in a single family of two tribes, the conifers may be conveniently distributed among five families, which agree, generally, in the following characters:—They are copiously branched trees or shrubs,

frequently of pyramidal form (as illustrated by the conventional "Christmas tree"—invariably a conifer). The leaves are always simple, and small compared with the size of the plant, usually linear, or short and scale-like, and generally persisting for more than one year. The plants are monoecious, e.g., *Pinus*, or dioecious, e.g., *Juniperus*, *Taxus*, and the cones are never terminal on the main stem. There is no perianth. The very regular monopodial branching is, perhaps, the most striking character of the majority of the conifers, of which a good example is seen in the giant Californian redwood, *Sequoia* (*Wellingtonia*) *gigantea*, the largest of the Gymnosperms, often seen in cultivation. Other conifers of this typical habit are many pines and firs, the monkey puzzle tree (*Araucaria imbricata*), the Norfolk Island pine (*Araucaria excelsa*), and the cedars and larches, several species exceeding 150 ft. in height. The yews and junipers and some other conifers grow as bushes, which in place of a main mast-like stem possess several repeatedly branched leading shoots. Dwarf forms are sometimes met with under arctic, alpine or other unfavourable conditions. Probably the smallest of these dwarf conifers is *Dacrydium laxifolium*, found on New Zealand moors, which may bear seed when only 2 in. high. Artificially dwarfed specimens of some species are commonly cultivated by the Japanese.

**Leaves.**—Nearly all conifers are evergreen and retain their leaves for from three to ten years; the larch (*Larix*), however, sheds its leaves each autumn, and those of the Chinese larch (*Pseudolarix Kaempferi*), which is also deciduous, turn a bright yellow before falling. In the swamp cypress (*Taxodium distichum*) the tree assumes a rich brown colour in the autumn, and sheds its leaves with the branchlets which bear them. Deciduous branches occur also in some other species. The leaves of conifers are usually characterized by their small size, e.g., the needle form represented by *Pinus*, *Cedrus*, *Larix*, etc., the linear flat or angular leaves, appressed to the branches, of *Thuja*, *Cupressus*, *Libocedrus*, etc.; all of which have a single median vein. The flat and comparatively broad leaves of *Araucaria imbricata*, *A. Bidwillii*, and a few species of the southern genus *Podocarpus*, are traversed by several parallel veins, as are the still larger leaves of *Agathis*, which may reach a length of several inches. In addition to the foliage leaves several genera also possess scale leaves of various kinds, represented by bud-scales in *Pinus*, *Picea*, etc., which frequently persist for a time at the base of a young shoot which has pushed its way through the yielding cap of protecting scales, while in some conifers the bud-scales adhere together, and after being torn near the base are carried up by the growing axis as a thin brown cap. The cypresses, Araucarias and some other conifers, have no true bud-scales; in some species, e.g., *Araucaria Bidwillii*, the occurrence of small foliage leaves, which have functioned as bud-scales, at intervals on the shoots,

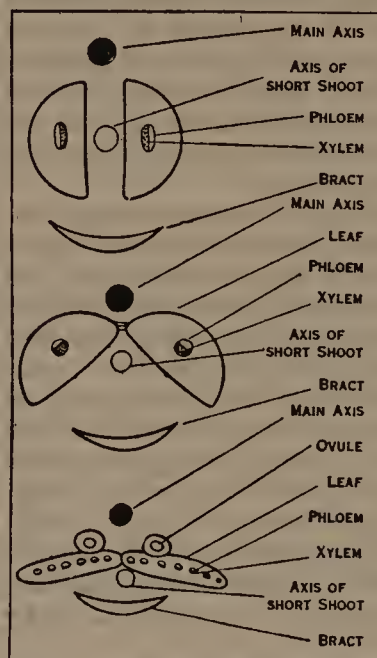


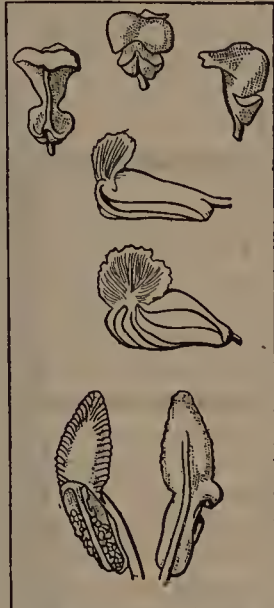
FIG. 12.—(A) NORMAL SHORT SHOOT OF PINUS. (B) "DOUBLE NEEDLE" OF SCIADOPITYS. (C) OVULIFEROUS SCALE OF LARIX OR PINUS

affords a measure of seasonal growth. The occurrence of long and short shoots is a characteristic feature of pines, cedars and larches. In *Pinus* the needles occur in pairs, or in clusters of three or five at the apex of small and inconspicuous short shoots of limited growth (spurs). The spur is enclosed at its base by a few scale leaves, and is borne on a branch of unlimited growth in the axil of a scale leaf. In some junipers, cypresses, etc., in which small leaves appressed to the stem are normal in adult plants, examples occur in which these leaves are replaced by the slender needle-like leaves, standing out more or less at right angles to the branch, which are characteristic of the seedling stage. Such cases are often



seen in cultivation, and are usually named "Retinospora," though this name does not denote a true genus, but merely the persistent juvenile forms of *Thuja*, *Juniperus*, *Cupressus*, and other trees of the same type.

A remarkable and unique leaf is found in the umbrella pine (*Sciadopitys verticillata*). These leaves are produced singly on whorls of spur shoots and bear traces, in the grooved surface and in the possession of two separate veins, of an origin from pairs of needle leaves. A peculiarity of these leaves is the inverse orientation of the vascular tissue; each of the two veins has its phloem next the upper, and the xylem towards the lower, surface of the leaf; this unusual position of the xylem and phloem is explained by regarding the needle of *Sciadopitys* as composed of a pair of leaves on a short shoot, fused by their upper margins (fig. 12). The short shoots of the cedar and larch are stouter structures bearing an indefinite number of leaves, and are not shed with the leaves as are the spurs of pines and *Sciadopitys*. In the genus *Phyllocladus* (New Zealand, etc.) there are no green foliage leaves, but in their place flattened branches (phylloclades) borne in the axils of small scale leaves. The cotyledons are usually two in number in conifers, but occasionally more, as in cedars and pines, reaching as many as 15 in the last named.



FROM ENGLER AND PRANTL, "DIE NATÜRLICHEN PFLANZENFAMILIEN" (ENGELMANN)

FIG. 13.—VARIOUS CONIFER MICROSPOROPHYLLS

**Cones.**—A typical "male" cone consists of a central axis bearing from less than a dozen to a very large number of sporophylls which usually follow the leaf arrangement, *i.e.*, they are generally spirally arranged except in most of the Cupressaceae where they are opposite or whorled. The sporophyll (fig. 13) is composed of a slender stalk, terminating in a knob or scale and bearing from two to 15 pollen-sacs on its lower surface. The larger number of sporangia (6 to 15) are characteristic of *Araucaria* (fig. 13) and *Agathis* in which the sporangia are also peculiar in their large size and in being long, narrow and free. They may thus be compared to the sporangia of the horse-tails (*Equisetum*). In the yew (*Taxus*) the stalk is attached to the centre of a large more or less circular expansion bearing four to eight pollen-sacs on its inner surface, but which are also fused with the stalk, not hanging freely like those of *Araucaria*. The sporangia usually open by a longitudinal, occasionally by a transverse, slit.

The structure of the "female" cone differs considerably in the five families of conifers which are as follows:—

- |                    |                                  |
|--------------------|----------------------------------|
| I. ARAUCARIACEAE.  | 2 genera and about 18 species.   |
| II. PODOCARPACEAE. | 7 genera and about 100 species.  |
| III. PINACEAE.     | 10 genera and about 200 species. |
| IV. CUPRESSACEAE.  | 22 genera and about 140 species. |
| V. TAXACEAE.       | 5 genera and about 12 species.   |

In the first family—Araucariaceae—the female cone, especially when young, has often a close resemblance to the male, and may be interpreted as homologous with it. On this view it is regarded as an axis bearing a large number of sporophylls, closely packed and spirally arranged. Each sporophyll consists of a scale-like basal part and a terminal up-turned leafy part—the lamina. Embedded in the scale with its apex facing the cone axis is a single large ovule. The nucellus is long and narrow and projects beyond the micropyle. In *Araucaria* (but not in *Agathis*) a *ligule* projects from the upper surface of the scale beyond the base of the ovule.

In the Podocarpaceae the cone is often much reduced, ranging from an axis with a small number of sporophylls, each bearing an inverted ovule, as in *Microcachrys*, *Saxegothea* (fig. 15), and some species of *Dacrydium*, to the form found in other species of *Dacrydium* and in *Podocarpus*, where the number of fertile scales is reduced to two or one, small in comparison with the large inverted ovules. In the latter case, broadly speaking, the cone practically

consists eventually of one or two naked ovules, though traces of the subtending scales can always be found. *Phyllocladus* and *Pherosphaera* are exceptional in having erect (not inverted) ovules. The ovules of the Podocarpaceae usually have a second, outer, integument, the epimatium, wholly or partially enclosing the inner (fig. 15).

The female cones of the third family, Pinaceae, are better known, but much more difficult to interpret. To this family most of the common northern conifers belong, such as the pines, spruces, silver firs, cedars and larches. The last-named will serve as a type. Here the cone consists of an axis bearing a large number of closely set, spirally arranged *pairs* of scales. Of the two scales in each pair one is immediately above the other (*i.e.*, in its axil), the lower being bract-like and sterile and known as the carpellary scale or *bract scale*, the upper bearing the ovules (usually two) on its upper surface and being known therefore as the *ovuliferous scale*. The small ovules are fused to the surface of the scale at its proximal end, and lie with their micropyles facing the axis. In the very young cone the two sorts of scales are of similar size; after pollination the ovuliferous scale grows considerably, and is always thicker than the subtending bract scale. The latter, in the larch, at first grows in length faster than the former and so projects beyond the ovuliferous scale in the older cone, but in most cases the bract scales either remain quite abortive after pollina-

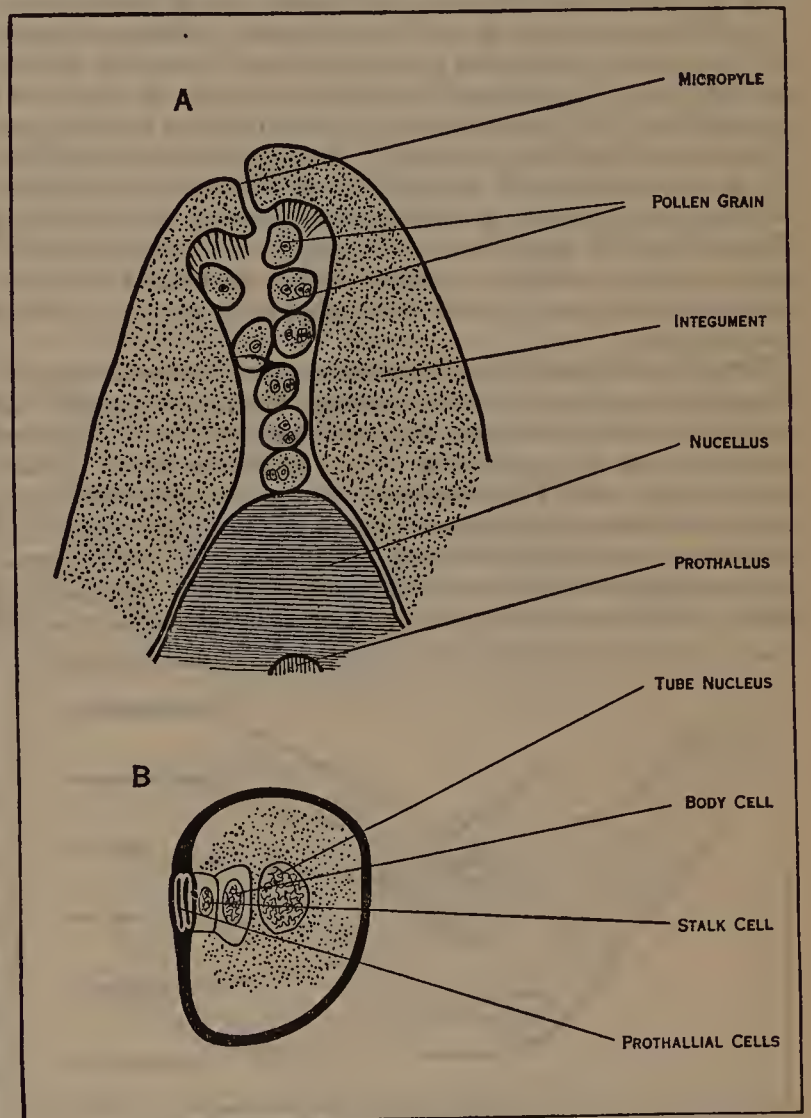


FIG. 14.—(A) MICROPYLE OF LARIX EUROPAEA FULL OF POLLEN GRAINS; (B) SINGLE POLLEN GRAIN FROM MICROPYLE OF LARIX EUROPAEA

tion, as in the pine, or grow much more slowly than the ovuliferous scales, the latter alone showing on the outside of the cone. In both cases the scales fuse together externally after pollination, forming a continuous outer covering to the cone and effectually enclosing the ovules, which remain hidden until after the seeds are ripe, often for one, two or more years.

It is not possible to explain here the various views which have been held as to the nature of the ovuliferous scale (the bract scale is clearly homologous with a subtending leaf) but that which



has been most generally accepted was due, in the first place, to Alexander Braun in 1842. He explained the ovuliferous scale as representing the two leaves of a spur shoot, fused (as in the double needle of *Sciadopitys*), by their posterior (adaxial) margins. The usual two ovules would thus be borne one on each leaf (sporophyll), as in the preceding families. This explanation also takes account of the *inverted vascular supply* of the ovuliferous scale, again paralleled in the leaf of *Sciadopitys* (fig. 12). In abnormal cones the ovuliferous scale is sometimes replaced by a dwarf shoot bearing two leaves, which lends further support to Braun's hypothesis.

In the next family, Cupressaceae, the more typical genera appear to have only one kind of scale, while others, belonging to the tribe Taxodioideae, often have a ligule-like structure on the upper surface of the scale (e.g., *Cunninghamia*). The ovules are borne close to the base of the scale, and are usually erect, less commonly inverted. The number borne on one scale is very variable, but from three to seven is usual. Anatomical examination of the scale, however, always indicates the presence of *two sets of vascular strands of which the upper is inverted*; of which the most obvious explanation is that the cone scale represents the bract and ovuliferous scales of the Pinaceae partially or wholly fused together. There are certain difficulties in this apparently simple explanation, but nevertheless it is a generally accepted view.

In the last family, Taxaceae, the female cone is an even more reduced structure than in the Podocarpaceae, consisting usually of a very short axis bearing few or many scale leaves at its base and apparently terminating in a single erect ovule. In reality the apparently terminal ovule may be in the axil of one of the uppermost scales. The whole structure is so reduced that it is difficult, and perhaps unprofitable, to explain it in terms of the other four families, but at least it gives little indication of the complexity characteristic of Pinaceae and Cupressaceae. Unlike cycads, *Ginkgo* and the majority of other conifers the ovule has two integuments, the outer more or less fleshy, as in the red "aril" of the yew seed.

**Fertilization and Development.**—The structure of the pollen grain is not identical in the different families of conifers, the differences partly concerning the prothallial cells, which are from two to several in number and form a persistent tissue in both Araucariaceae and Podocarpaceae (except *Pherosphaera*), two and quite ephemeral in Pinaceae (except in *Sciadopitys* where they are absent), and entirely wanting in Cupressaceae and Taxaceae. The remaining divisions in the pollen grain and tube correspond to those in cycads and *Ginkgo*, i.e., a tube nucleus and generative cell

ovule and on evaporation of which the pollen is drawn down to the apex of the nucellus. The pollen tube at once begins to grow into the nucellus, but downwards, towards the prothallus, not laterally as in cycads, and into the tube pass, not only the tube nucleus but also, in all cases, the stalk nucleus and body cell. No

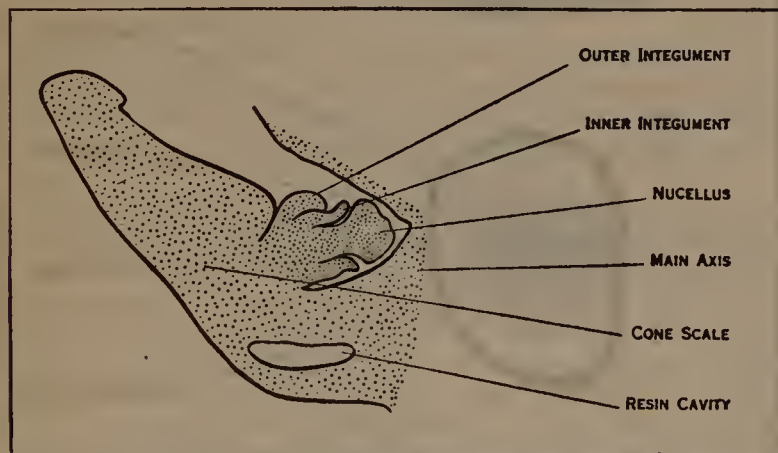


FIG. 15.—SCALE AND OVULE OF SAXEGOTHEA

are formed, after which the pollen is usually shed (though this may happen before these cells are differentiated as in *Widdringtonia* or after the division of the generative cell to form stalk and body cells as in *Larix* and most Pinaceae [fig. 14]). The pollen is carried by the wind to the neighbourhood of the ovule. In Araucariaceae it germinates on the scales of the female cone, the tube eventually growing into the nucellus; in *Saxegothea* (Podocarpaceae) it germinates on the stigma-like apex of the nucellus (fig. 15), and in most other conifers it is caught in the *pollination drop* which is extruded from the open micropyle of the young

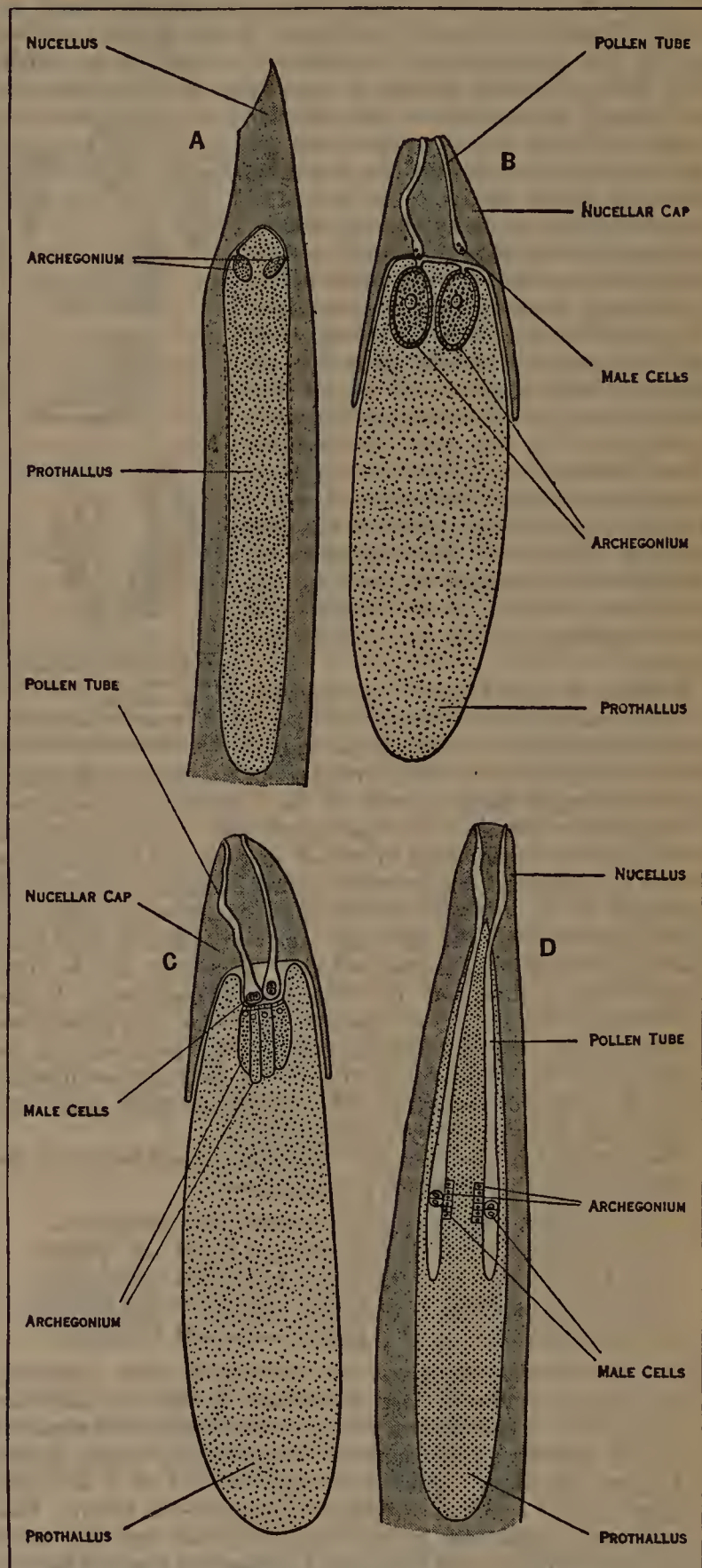


FIG. 16.—SEMI DIAGRAMMATIC LONGITUDINAL SECTIONS OF PROTHALLUS WITH NUCELLUS (OR NUCELLAR CAP) OF ARAUCARIA (A), PINUS (B), TETRCLINIS (C) AND ACTINOSTROBUS (D)

well organized pollen chamber is formed in the nucellus of conifers, but sometimes a few cells at its upper end break down and so produce a saucer-shaped depression (fig. 16). The body cell divides to form two *non-motile* male cells, which in Cupressaceae are exactly equal and both functional, but in the other families are usually unequal, and only the larger functional.



In the young ovule a single functional megaspore develops, usually the lowest of a row of three or four, formed from a mother-cell as in cycads and practically all other seed plants. Exceptionally, as in *Taxus*, *Callitris* and *Pherosphaera*, two or more megaspores may begin to develop. The formation of the prothallus takes place almost exactly as in cycads, but it is smaller, usually much smaller, in the conifers, as are also the archegonia. The latter are few, and formed (as in cycads) from separate superficial cells at the apex in Podocarpaceae (except *Pherosphaera* and *Microcachrys*), Pinaceae and Taxaceae (fig. 16); rather more numerous and more scattered, and more or less lateral, in *Pherosphaera* and in Araucariaceae (fig. 16), and in a single apical complex of 6 to 24 (all in contact with other archegonia of the group) in *Microcachrys* and in most Cupressaceae (fig. 16). In the remaining Cupressaceae, including *Sequoia* and the tribe Callitroideae, the archegonia are very small and numerous, usually deep-seated, and arranged in from one to several groups (in contact with each other in any one group) placed laterally along the prothallus, and never at, or very close to, the apex, which is usually pointed (fig. 16). The number of such archegonia may be up to about 60 in *Sequoia* or as many as 100 in *Widdringtonia*. A curious feature of these forms is that the size of the egg nucleus is about the same as that of the male nucleus at the time of fertilization, and in *Actinostrobus* (fig. 16) even the whole archegonium may be no larger than the male cell, so that we have here what practically amounts to a case of *isogamy*, of which no other example can be found in any plant of higher organization than the Algae and Fungi. It should be noted that in all conifers, in marked contrast with the preceding divisions, the male cells possess no cilia, and are carried by the growth of the pollen tube either into the archegonium itself or to a point very close to it. It is usual to describe the male cells as non-motile, but it is not clear that this is always strictly accurate as they may pass from the tube into the archegonium without being actually carried into it, which seems to imply some limited power of independent movement, possibly of an amoeboid nature. In the Araucariaceae, as in *Sequoia* and the Callitroideae, male and female nuclei are equal in size at the time of fertilization. In most other conifers the male nucleus is distinctly smaller than the female, while in the family Pinaceae it is only about one-hundredth of the volume of the female nucleus.

In conifers the neck of the archegonium is always composed of more cells than the two characteristic of cycads, but the actual number varies widely, from about four in one tier to about a dozen or more in several tiers. Speaking generally it is less conspicuous in the Cupressaceae than in the other families.

The early development of the embryo varies a good deal in the different families. In *Araucaria* and *Agathis* 32 or more free nuclei are formed in the protoplasm of the archegonium. These nuclei then arrange themselves into a central group (of two tiers) and a peripheral enveloping layer, after which walls are laid down between them. The structure thus formed is the proembryo and completely fills the archegonium. The central group alone forms the embryo, the basal cells of the peripheral layer functioning as a protective cap while the cells nearest the neck elongate to form a suspensor.

The case of the Pinaceae is best known. Here only four free nuclei are formed which pass to the base of the archegonium and there divide to form a basal layer of four cells and an upper tier of four nuclei. The latter repeat the process, resulting in two layers of cells and one of four nuclei above. Lastly the cells of the lowest tier divide once more giving three tiers of four cells each with one above of four nuclei. This is the structure of the proembryo and it occupies approximately the basal one-third or one-quarter of the archegonium. The tier of nuclei has no obvious function, the next tier may serve to prevent the suspensor cells growing back into the archegonial cavity, the lowest tier but one elongates enormously, forming the suspensor, while the basal tier forms the true embryo. The latter eventually becomes differentiated into a hypocotyl terminating in a radicle at the suspensor end and a whorl of, usually, several cotyledons at the other end, surrounding a central plumule. It sometimes happens that the four suspensor cells become separated from one another, along

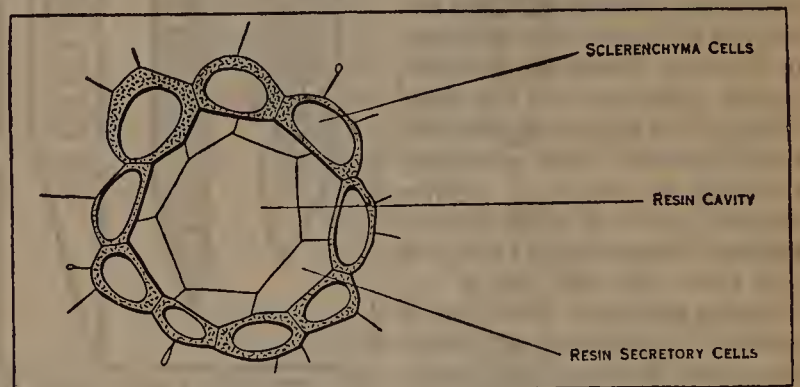
with the corresponding embryo cells, the latter then forming four separate embryos instead of one, though in any case not more than one embryo in a prothallus normally reaches maturity.

In the Podocarpaceae and in the more typical Cupressaceae (excluding *Sequoia* and the Callitroideae) proembryo development is similar to that in Pinaceae except that eight free nuclei are formed before cell formation and that the tiers are much less regular both in number and arrangement, the basal often consisting of only a single cell; and the embryo has usually only two cotyledons. In both cases the proembryo only occupies the basal part of the archegonium. The family Taxaceae only differs from the two preceding in the fact that the proembryo fills the archegonium, with the exception that the genus *Cephalotaxus* develops a protective cap like that of Araucarians.

In *Sequoia* and the Callitroideae cell formation takes place earlier than in any other forms (in *Sequoia* at the first division) and the proembryo fills the archegonium. The embryo develops from a single cell which may be that at the base of the archegonium (*Sequoia*) or may be cut off, at the end facing the base of the prothallus, from any of the lower cells of the proembryo (*Actinostrobus*). In either case the larger cell adjacent to the embryo cell becomes the suspensor.

In spite of these marked differences in the early embryo development there is a considerable uniformity in the structure of the seed in conifers. In most cases the testa ripens dry and woody, as the outer fleshy layer of the cycads only develops to a very small extent and finally withers away. Within the testa the nucellus is scarcely noticeable except as the withered remains of the nucellar cap, while the prothallus is always packed full of starch and so becomes somewhat brittle. The embryo normally lies symmetrically in the centre of the prothallus and is about two-thirds of its length and perhaps about one-tenth of its volume. In several conifers the seeds are winged, but while the wing is formed, in Pinaceae, from part of the tissue of the ovuliferous scale, in Cupressaceae (when present) it is part of the integument of the ovule (e.g., *Widdringtonia*). In Taxaceae and some Podocarpaceae the seeds have a fleshy covering, not always of the same nature, and in *Microcachrys* (Podocarpaceae) the cone scales themselves become fleshy, thus forming a "fruit" something like a small raspberry. In the juniper also (Cupressaceae) the fertile scales become fleshy, thus forming a berry-like "fruit."

**Anatomy.**—One of the most striking features of conifer anatomy is the occurrence of long cylindrical intercellular spaces lined with thin-walled, resin-secreting cells and known as resin-canals. These are frequently present in all parts of the plant and are never entirely absent except in *Taxus* and in *Dacrydium laxifolium*. In the former isolated resin-secreting cells occur here and



FROM ENGLER AND PRANTL, "DIE NATÜRLICHE PFLANZENFAMILIEN" (W. ENGELMANN)

FIG. 17.—RESIN CANAL IN PINUS SYLVESTRIS LEAF

there in the tissues, but in the latter even these appear to be lacking. The resin canals are most frequently found in the cortex and have a characteristic structure, the epithelial cells which secrete the resin being in turn surrounded, as a rule, by a ring of much more conspicuous thick-walled protecting cells (fig. 17). In many genera resin canals are also found in the wood, as in *Pinus*, while sometimes they are restricted to the cone axis, as in *Sequoia*. They are nearly always present in the leaves, often below the vascular bundle. Although resin canals are a characteristic feature of the conifers they are by no means peculiar to them, being equally



distinctive of some tropical families of flowering plants (e.g., Anacardiaceae) and occasional plants outside those families such as sunflower and ivy.

The phloem always includes sieve tubes without associated companion cells (though phloem-parenchyma cells with albuminous contents are present, and with pitted areas chiefly on their lateral walls). In the Pinaceae the phloem consists solely of sieve tubes and phloem parenchyma, but in most other forms concentric cylinders of bast fibres occur in regular alternation with the functional phloem.

Coniferous wood is homogeneous in structure, consisting almost entirely of tracheids with circular (rarely polygonal) bordered pits on the radial walls. Xylem parenchyma is never abundant, but traces of it are present in many genera. In *Pinus* there is no wood parenchyma except in association with the numerous resin canals scattered through the wood. The medullary rays consist of a single layer of cells except in certain Pinaceae (where some of them are fusiform in section, enclosing a single horizontal resin canal) and have usually a complex structure. The margins, both upper and lower, of that part of the ray which lies in the xylem, are often composed of horizontally elongated tracheids with irregularly folded walls and bordered pits, while the central rows of cells are parenchymatous and thin-walled, but usually pitted. In the phloem the marginal ray tracheids are replaced by irregularly lobed albuminous cells.

**Root.**—The roots of many conifers possess a narrow band of primary tracheids with a group of slender protoxylem elements along either margin (diarch). In other cases the primary xylem is triarch or tetrarch (*Sequoia*) or even polyarch. An old root approximates closely to a stem in structure, but the annual rings are often less clearly marked and the tracheids larger and thinner-walled. The primary tissues are, of course, differently arranged, but are apt to become obliterated with age.

**Stem.**—The primary vascular bundles in a young conifer stem are collateral, and, like those of a Dicotyledon, they are arranged in a circle round a central pith and enclosed by a common endodermis. Secondary thickening begins at an early stage and continues throughout the life of the plant with seasonal variations and interruptions resulting in the normal appearance of clearly defined annual rings, as in most woody Dicotyledons. The differences of structure met with in conifer stems are sometimes affected by the conditions (including climate) under which they are grown, and are more often distinctive of species than of genera or families. There are, however, certain characters of the wood which are of greater significance.

For instance the secondary tracheids of nearly all conifers (fig. 18) have a single row of separate bordered pits (rarely of two rows with the pits of the two rows opposite). This type of wood is distinctive of Podocarpaceae. Pinaceae and Cupressaceae. In *Araucaria* (fig. 18) and *Agathis* the bordered pits are in one, two or three rows on the radial walls and, being in contact, are polygonal in shape, and the pits of adjacent rows are alternate and not opposite. In *Taxus* (fig. 18) the normal type of bordered pit occurs, but in addition conspicuous spiral thickening-bands are met with. It is doubtless these which give to the wood of the yew its well-known strength and elasticity, recognized by the mediaeval English when they used it for their bows, which were the most efficient weapons of that period.

**Leaf.**—The cotyledons have each a single vascular strand ex-

cept in *Podocarpus*, which has two, and in Araucarians where there are four or more. In the latter there are also several resin canals, one or two of which are also found in *Pinus*, though absent in most other forms. The adult leaves (fig. 20) have a single median vein except in *Agathis*, several species of *Araucaria* (fig. 20 C) and a few of *Podocarpus*, which have several parallel veins. In some pines (e.g., *Pinus* and *Abies* [fig. 20]) this vein includes two vascular bundles, but in others, and in all

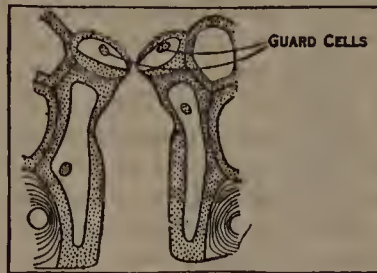
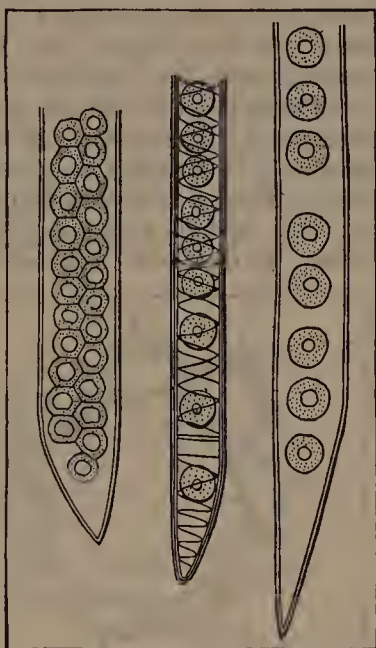


FIG. 19.—STOMA OF *PINUS SYL-VESTRIS*

Cupressaceae (fig. 20) and Taxaceae and in all podocarps, except the few species of *Podocarpus* already mentioned, there is only a single vascular strand. In all cases the leaf trace leaves the central cylinder as a single strand, unlike *Ginkgo* and the cycads, but in *Araucaria*, etc., this strand splits into several in its passage through the cortex. In most genera one or more resin canals are found in the leaf, and another equally distinctive feature is the presence, generally on the flanks of the vascular strand, of a few isodiametric tracheids known as "transfusion tracheids." Sometimes there are also horizontally elongated transfusion tracheids extending towards the leaf margin. A noteworthy feature is the common occurrence of hypodermal fibres, but their presence and extent is partly dependent on the light conditions under which their development takes place; e.g., a pine needle grown in continuous light lacks the usual hypodermal fibres, as well as differing in some other details. In *Pinus* and *Cedrus* the homogeneous mesophyll is characterized by the infolding of the cell walls. In many leaves, such as those of *Abies* (fig. 20) and *Larix* there is both palisade and spongy parenchyma. In *Araucaria imbricata* (fig. 20) a palisade layer occurs in both upper and lower parts of the mesophyll, and resin canals are found between the veins, while in the multi-nerved species of *Podocarpus* (section *Nageia*) a canal occurs below each vein. This position (below the vein) is that usual for the single resin canal of many forms (fig. 20), while in *Larix*, *Abies*, etc., two canals run through the leaf parallel to the margins (fig. 20). Each stoma is normally sunk at the base of a pit (fig. 19), and the stomata are frequently arranged in rows, their position being marked by two or more bands of wax on the surface of the living leaf.

**Geographical Distribution.**—Most conifers grow in forests, either alone or mixed with angiospermous trees, forming one of the characteristic features of the vegetation in temperate and alpine regions. Since a large proportion of the cold temperate lands lies in the northern hemisphere it is easy to understand why the chief home of the Coniferales is in the north, where certain species occasionally extend into the arctic circle and beyond the tree limit, e.g., *Juniperus nana*. The tree limit in northern Europe is chiefly marked by conifers (*Picea*, *Larix*, *Abies*, *Pinus*, etc.), and many are abundant in North America, such as *Juniperus virginiana*, *Taxodium* and several pines on the eastern side; *Pseudotsuga*, *Sequoia*, other pines, etc., on the west; while *Picea*, *Larix*, *Abies*, *Tsuga*, *Taxus* and *Pinus strobus* are characteristic forms throughout. In the Mediterranean region occur *Pinus maritima*, *P. pinea* and other species, cedars and cypresses. In Japan and China are a number of small endemic genera such as *Cryptomeria*, *Cunninghamia*, *Sciadopitys*, *Cephalotaxus* and *Pseudolarix*. In the Himalayas are *Cedrus*, *Taxus* and endemic species of *Abies*, *Pinus*, etc. Apart from high altitudes few conifers are found in the tropics, but various endemic types are met with in the south, of which *Podocarpus* is most widely distributed, while *Widdringtonia* is peculiar to South Africa and a considerable number of characteristic genera are found in Australasia, such as *Callitris*, *Agathis*, *Dacrydium*, *Microcachrys*, *Athrotaxis* and *Araucaria*, most of which are endemic. The last named, however, occurs in South America as well, where *Fitzroya* and *Saxegothea* are also met with, chiefly in the Andes.

**Classification.**—In conclusion a brief account of the characters of the five families and their tribes, and a key to the principal genera of each may be given:



FIGS. FROM BAKER & SMITH, "PINES OF AUSTRALIA"

FIG. 18.—TRACHEIDS: *ARAUCARIA* (LEFT); *TAXUS* (CENTRE); *PINUS* (RIGHT)



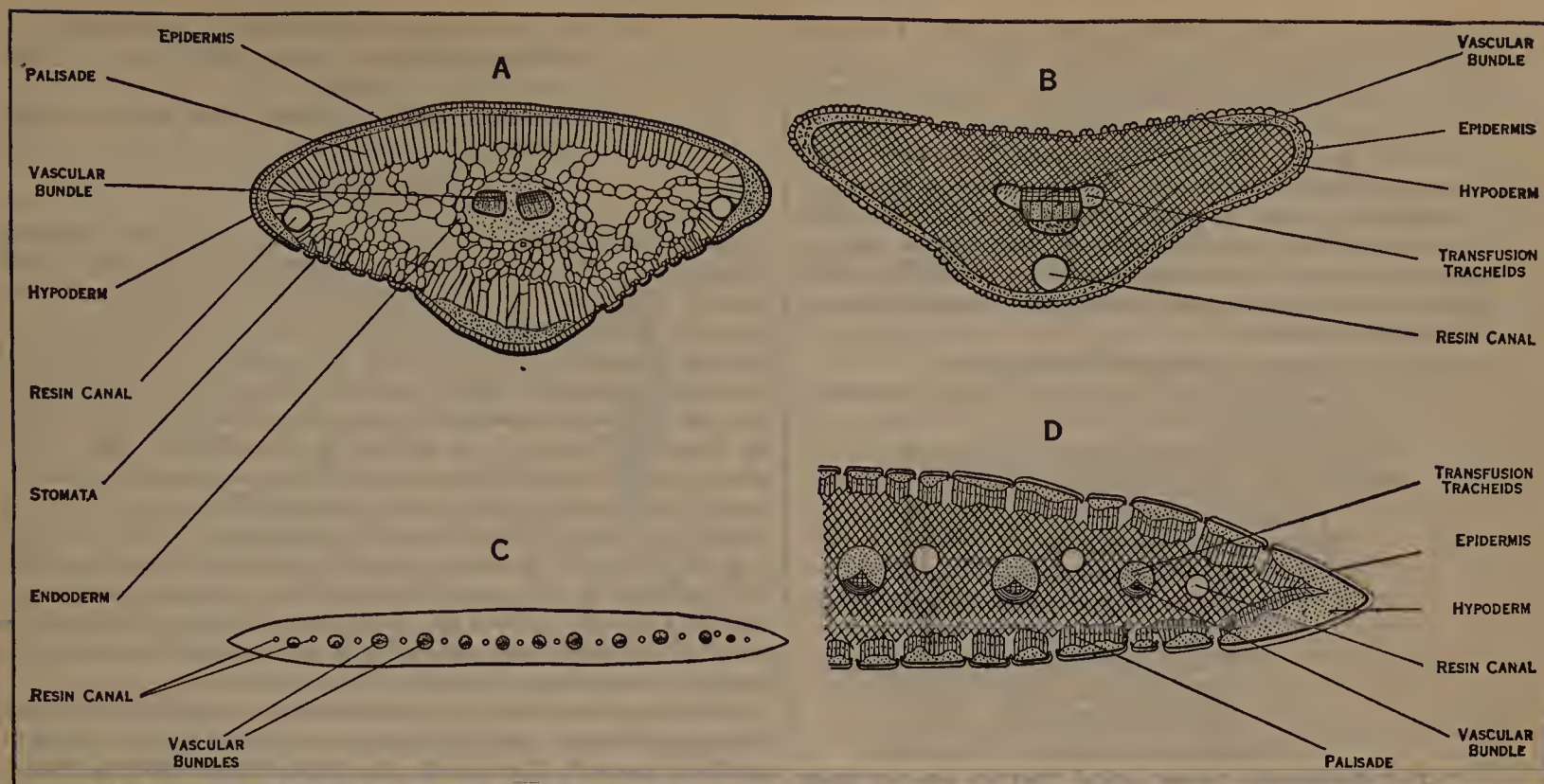


FIG. 20.—(A) LEAF OF *ABIES PUNGENS*; (B) *JUNIPERIS COMMUNIS*; (C) *ARAUCARIA IMBRICATA*; (D) PART OF *ARAUCARIA IMBRICATA* ON LARGER SCALE

I. **ARAUCARIACEAE.** Large trees. Both male and female cones rather large. Microsporophylls with numerous long, narrow, pendulous pollen sacs. Megasporophylls numerous, simple and bearing solitary ovules embedded in the tissue. Nucellus extending beyond the integument. Prothallus with separate scattered archegonia, usually more or less lateral. Several prothallial cells in the pollen grain. Tracheids with multiseriate pitting.

\*Dioecious. Megasporophyll with a ligule. *Araucaria*.

\*\*Monoecious. Megasporophyll without a ligule. *Agathis*.

II. **PODOCARPACEAE.** Trees, shrubs and small undershrubs, mostly dioecious. Megasporophylls not numerous in the cone, each bearing a single, usually inverted ovule. Male cones with spiral or sometimes whorled sporophylls, each with two pollen sacs. Pollen often winged, with a group of two or more persistent prothallial cells (except in *Pherosphaera*). Archegonia separate, each with its own jacket cells, as in *Araucariaceae*, but apical, not lateral (except in *Pherosphaera* and *Microcachrys*).

\*Flat expanded branches and no true foliage leaves.

Ovules erect. *Phyllocladus*.

\*\*Normal foliage leaves.

†Megasporophylls solitary or in pairs, or a few very laxly arranged on a strobilus, but never joining to cover the more or less inverted ovules.

○Pollen winged. Ovules always fully inverted, on a swollen stalk and solitary or in pairs. *Podocarpus*.

○○Pollen not winged. Ovule sessile and not fully inverted. *Dacrydium*.

††Megasporophylls in a cone, growing together so as to enclose the ovules.

○Ovules more or less inverted. Epimatium present.

§Monoecious. Leaves needle-like. *Saxegothea*.

§§Dioecious. Leaves scale-like. *Microcachrys*.

○○Ovules erect and axillary. No epimatium. *Pherosphaera*.

III. **PINACEAE.** Trees and shrubs, usually monoecious. Male

cones like those of *Podocarpaceae*, with two pollen sacs to each sporophyll. Female cone compact with many pairs of scales, the upper of each pair bearing two, or rarely more, ovules. Archegonia separate, each in its own jacket cells, as in *Podocarpaceae*.

A. Pollen with no prothallial cells. A single grooved leaf on each short shoot with two veins, one either side of the groove. Several ovules on the ovuliferous scale. Tribe 1. *Sciadopitoideae*. *Sciadopitys*.

Except for the separate archegonia, could be equally well placed in the *Cupressaceae*.

B. Pollen with two ephemeral prothallial cells. Leaves with a single vein. Two ovules on each ovuliferous scale. Tribe 2. *Abietoideae*.

(i.) Leaves almost entirely borne on spur shoots.

\*From one to five leaves (the number more or less constant in each species) on each short shoot. *Pinus*.

\*\*A tuft of more than five leaves on each spur shoot.

†Leaves not deciduous. *Cedrus*.

††Leaves deciduous.

○Cone scales deciduous. Rim of micropyle spreading. Pollen winged. *Pseudolarix*.

○○Cone scales persistent. Rim of micropyle infolded. Pollen not winged. *Larix*.

(ii.) Leaves borne on branches of unlimited growth.

\*Bract scales three-lobed, and projecting beyond the ovuliferous scales. Rim of the micropyle infolded. *Pseudotsuga*.

\*\*Bract scales not three-lobed even when longer than the ovuliferous scales. Rim of the micropyle spreading.

†Cones pendulous. Cone scales persistent.

○Pollen sacs dehisce longitudinally.

Pollen winged. Cones large. *Picea*.

○○Pollen sacs dehisce transversely.

Pollen globose. Cones small. *Tsuga*.

††Cones erect. Cone scales deciduous. Bract scales often longer than the ovuliferous scales. Leaves flat. *Abies*.



IV. CUPRESSACEAE. Trees or shrubs, often dioecious. Only one kind of scale in the female cone as a rule, but sometimes with outgrowths on the upper surface. Number of fertile scales usually much smaller than in Pinaceae, often only from two to six or eight. Ovules inverted or more often erect, commonly more than two to each fertile scale. Archegonia in one or more *groups*, not solitary. Male cones small with usually three or more pollen sacs to each sporophyll. Pollen grain without prothallial cells. Leaves usually small, not infrequently dimorphic, as in *Juniperus chinensis*.

A. Leaves opposite or whorled. Ovules erect.

(i.) Archegonia in a single apical group. Tribe 1. Cupressoideae.

\*Cone scales ripening fleshy. *Juniperus*.

\*\*Cone scales ripening woody.

†Cone scales peltate. *Cupressus*.

††Cone scales not peltate.

°Cone scales imbricate.

a. Four or five seeds to each scale.

*Thujopsis*.

β. Usually two seeds to each scale.

§Two fertile scales. *Libocedrus*.

§§Four fertile scales. *Thuja*.

°°Cone scales valvate. *Tetrclinis*.

(ii.) Archegonia never apical, but in one or more lateral groups, usually deep-seated. Tribe 2. Callitroideae.

\*Scales slightly imbricate (imperfectly known; may prove to belong to the preceding tribe). *Fitzroya*.

\*\*Scales valvate.

†Fertile scales four in decussate pairs. *Widdringtonia*.

††Fertile scales six in alternating whorls of three.

°Cone with a number of sterile bracts at the base. Fertile scales all equal. *Actinostrobus*.

°°No sterile bracts at base of cone. Fertile scales unequal. *Callitris*.

B. Leaves spirally arranged.

(i.) Archegonia in a single apical complex. Tribe 3. Taxodioideae.

\*Leafy branchlets deciduous. *Taxodium*.

\*\*Leaves, cone-scales deciduous. *Glyptostrobus*.

\*\*\*Neither leaves nor branchlets deciduous.

†Seeds erect. *Cryptomeria*.

††Seeds inverted.

°Fertile scales with a narrow transverse membrane (ligule) above the seed. Leaves lanceolate. *Cunninghamia*.

°°Fertile scales with a transverse ridge above the seed. *Athrotaxis*.

(ii.) Archegonia never apical. Tribe 4. Sequoioideae. *Sequoia*.

It is quite possible that tribes 3 and 4 above should be merged in tribes 1 and 2 respectively, the distinction based on the leaf arrangement being probably unimportant, and not always constant.

V. TAXACEAE. Small trees and shrubs, usually dioecious, with much reduced female cones often consisting of single naked erect ovules subtended by a number of bracts, the ovules usually with an outer fleshy integument. Archegonia as in Pinaceae. Male cones small with peltate or crested sporophylls each bearing from two to seven, or more pollen sacs. Pollen grains without prothallial cells. Leaves usually free and blade-like.

\*One or two erect ovules borne on a small fleshy fertile scale which becomes abortive as the seeds ripen. No aril. *Cephalotaxus*.

\*\*“Cone” reduced to a naked ovule. Aril present.

†Microsporophylls crested, with two to four pollen sacs. *Torreya*.

††Microsporophylls peltate with four to eight pollen sacs. *Taxus*.

### GNETALES

These are perennial, normally dioecious plants with opposite simple leaves. The perianth of one or two whorls is distinctive, and sharply contrasts this division with other Gymnosperms. The cones are more complex than in other forms, consisting of an axis bearing decussate pairs of bracts or a number of superposed whorls of bracts, each whorl connate in a cup-like form. In either case the ovulate or staminate structures, which for convenience we may call “flowers,” are axillary to these bracts. The flower always consists of one or two pairs of free or connate scales, the perianth, enclosing either a single ovule with a long projecting micropylar tube, or from one to six stamens. It is evident that it is the *flowers* of Gnetales, especially the female flowers, which are equivalent to the cones of conifers (e.g., compare the female cone of *Torreya*) and not the whole “cone,” which might well be called a compound cone, and which is also comparable to the catkin-like inflorescence of certain flowering plants.

In their anatomy also the Gnetales show a marked resemblance to angiosperms, as, though the phloem remains typical of gymnosperms in general, true vessels, like those of the flowering plants, are associated with typical gymnospermous tracheids in the wood, and there are no resin canals.

The division includes only three genera, which are so entirely unlike in appearance as to suggest at first sight that each must be regarded as the type of a separate family. But detailed study of development and anatomy has indicated a very close similarity in the former respect between two of the genera, and at least a partial explanation of their complete dissimilarity in appearance, while emphasizing the divergence of the third. They are therefore considered here as forming *two* families, as follows:—

I. EPHEDRACEAE. Much branched small-leaved xerophytic shrubs. Ovule with two integuments containing a prothallus with archegonia, similar to that of conifers. *Ephedra*.

II. GNETACEAE. Vegetative region of the plant unbranched or sparingly branched. Ovule with one or two integuments and containing a prothallus which does not form archegonia. Leaves large.

A. Tribe Welwitschioideae. Plant tuberous and chiefly underground, developing only two enormously long and straggling, parallel-veined leaves after the cotyledons. *Welwitschia*.

B. Tribe Gnetoideae. Plant a tree or large woody climber, with numerous net-veined leaves indistinguishable from those of ordinary dicotyledons. *Gnetum*.

It seems evident that *Ephedra*, both in general habit and in the possession of archegonia is intermediate in character between the conifers (having points of resemblance to both Cupressaceae and Taxaceae), and the Gnetaceae, while *Gnetum* has many points of similarity to the true flowering plants. Most botanists have hesitated (no doubt rightly) to look upon the Gnetaceae as the direct ancestors of the flowering plants, but it is not altogether unlikely that both may have originated from the same stock, which was perhaps not very different from *Gnetum*. It is indeed a very surprising fact that the geological history of the Gnetales is unknown.

*Ephedra* is the largest genus of Gnetales, with about 35 species, and the only one represented in Europe. It is confined to more or less arid warm-temperate and tropical regions and one species is common on sand dunes along parts of the Mediterranean coast. The finer branches are green; the surface of the long internodes is marked by fine longitudinal ribs; and at the nodes are borne pairs of small, partially connate scale leaves, the general appearance being similar to that of a stem of *Equisetum* or a twig of *Casuarina*. Some of the branches bear pairs of small cones in the axils of the scale leaves. The cone scales are broad and imbricate. Each male flower (fig. 21) consists of an inconspicuous



perianth, composed of two more or less concrescent bracts, enclosing an axis projecting beyond the perianth and terminating in two (sometimes more, up to six or eight) sporangia. The resemblance of this structure to a stamen is obvious, but it is no less clearly homologous with the microsporophyll of conifers.

The female flower is enveloped in a closely fitting perianth of two more or less connate bracts, as in the male flower. This perianth encloses a single ovule with two integuments, the inner, which is not more than two cells thick, prolonged upwards as a beak-like micropyle, the outer, which is thicker and later becomes woody, only reaching about half way up the micropylar beak. The micropyle secretes a pollination drop, as in conifers.

A prothallus is organized exactly as in conifers, the two to five archegonia being developed from separate superficial cells at the apex, and having long, multicellular, necks. About the time when they first appear the tip of the nucellus begins to break down, this disorganization proceeding downwards until there is (when the archegonia are mature) a broad circular pollen chamber open to the top of the prothallus, thus permitting the pollen grains to rest on the necks of the archegonia. The development of the pollen grain is closely similar to that of *Larix* and it is shed in the 5-nucleate condition. Division of the body cell occurs immediately after pollination and the pollen tube forces its way between the neck cells and discharges its contents into the egg within a few hours. The fusion nucleus divides three times to form eight nuclei, some of which then become organized into walled cells, very loosely connected into a proembryo. Each of these cells, after division of its nucleus, elongates and cuts off a small embryonal cell containing one of the two nuclei, the larger cell remaining, the suspensor, elongating rapidly to thrust the embryo cell deep into the prothallus tissue. The embryo cell divides to form an ovoid mass of cells of which those next to the suspensor elongate in succession giving rise to embryonal tubes which add to the length of the suspensor. The whole process is strongly reminiscent of what takes place in *Actinostrobus* among the conifers. This description applies more particularly to *Ephedra trifurca*, and it is uncertain how far the embryo development of other species agrees with it. In any case only one embryo matures.

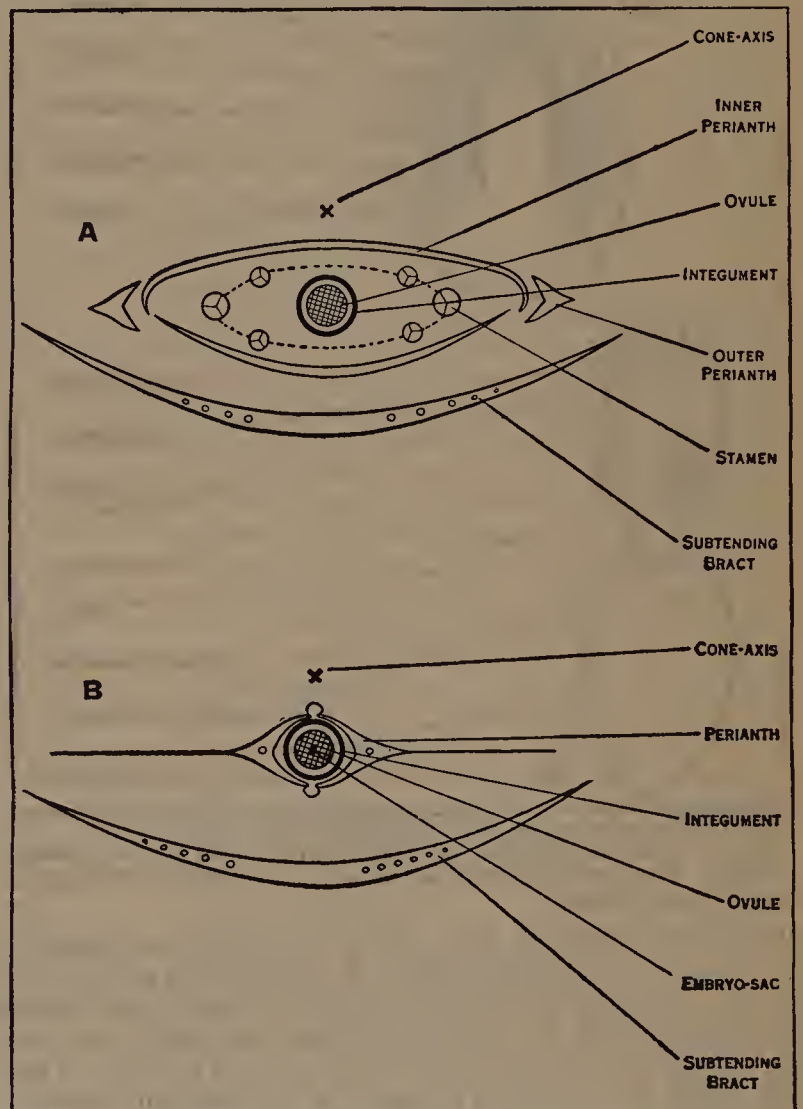
**Welwitschia.**—*W. mirabilis* is the only species of this remarkable genus and is found in two isolated and restricted areas of the coastal desert region of Damaraland in South-west Africa. It is by far the most remarkable member of the Gnetales not only in its habit but also both in the form of its flowers and the details of its development. Knowledge of these details is largely due to investigations carried out by H. H. W. Pearson. An adult plant has somewhat the form of a gigantic radish two to four feet in diameter, projecting less than a foot above the ground, and terminating in a long tap-root below. The two strap-shaped leaves trail along the ground to a length of roft. or more, and become split into a number of narrow thong-like strips. They retain the power of growth at the base throughout the life of the plant which probably exceeds 100 years. The characteristics of the plant accord well with the interesting suggestion that it may represent an "adult seedling." Numerous circular pits occur on the concentric ridges of the depressed and wrinkled crown, marking the positions of former inflorescences, new ridges subsequently appearing outside the old ones. The inflorescences have the form of dichasially branched stalks bearing the cones, from one to 20 in the female plant and up to 50 in the male. The female cone is about an inch long and scarlet in colour, the male smaller and more slender. Each consists of an axis bearing a large number of alternating pairs of overlapping bracts, in the axils of which are the flowers. The staminate flower (fig. 22) is enclosed by a perianth of two opposite pairs of bracts, surrounding a ring of six stamens united below but free above and each terminating in a trilobular anther. In the centre of the flower is an abortive ovule the integument of which projects upwards as a spirally



FROM ENGLER & PRANTL, "DIE NATÜRLICHEN PFLANZENFAMILIEN" (WM. ENGLEMANN)

FIG. 21.—MALE FLOWER OF *EPHEDRA FRAGILIS*

twisted tube with a stigma-like expansion at its apex. In the development of the pollen grain, a single prothallial nucleus is cut off, which disappears again about the time of pollination. There are only two further divisions resulting in a tube nucleus and two male nuclei, the formation of a stalk cell which occurs without exception in all conifers, as well as in *Ephedra*, being omitted. There is evidence that pollination is effected by insect agency. The ovulate flower consists of an erect ovule with two investments of which the outer is winged and represents the perianth, formed of a pair of completely connate bracts, the inner being the integument which has the usual long tubular micropyle (fig. 22). No pollen chamber is formed, but numerous pollen tubes grow downwards in the nucellar cap. The megaspore begins to develop as usual, becoming filled with protoplasm containing over 1,000 nuclei before walls appear. The latter divide the whole sac into multinucleate compartments, those in the micropylar end containing fewer and larger nuclei, any of which may function as eggs. The remainder contain about a dozen nuclei each, all of which fuse together in the compartment, thus forming a tissue of uninucleate cells which then grows considerably and may be termed the endosperm. The micropylar multinucleate cells put out long tubes which grow upwards into the nucellar cap, and into which the egg nuclei pass. These ascending prothallial tubes meet, and fuse with the descending pollen tubes and at the point of



FROM H. H. W. PEARSON, IN THE PROCEEDINGS OF THE ROYAL SOCIETY

FIG. 22.—WELWITSCHIA: CROSS-SECTION OF FLORAL STRUCTURES. A. MALE FLOWER; B. FEMALE FLOWER

fusion, fertilization occurs. The fertilized egg forms a wall and elongates into a tube from which an embryo tip cell is cut off, the remainder of the tube being the suspensor which carries the embryo deep into the endosperm. The further development is similar to that in *Ephedra*, including the formation of embryonal tubes from the young embryo.

**Gnetum** is represented by about 30 species, mostly climbers, found both in tropical America and in tropical regions of the Old World. The oval leaves are two or three inches long and are borne



in pairs at the swollen nodes. The cones are long and cylindrical and bear whorls of flowers at each node, accompanied by numerous sterile hairs, in the axils of cup-like concrescent bracts. In a male inflorescence very numerous flowers may be found, up to about 3,000 in one species, while in a female spike the number of flowers probably does not reach 100. The staminate flower consists of a perianth of two concrescent bracts enclosing a

nucleate "cells," the nuclei of each cell subsequently fusing so that an endosperm of uninucleate cells results, into which the developing embryos penetrate. Each zygote of *G. Gnemon* is stated to elongate and form a long tortuous multinucleate suspensor, from the lower end of which a small, also multinucleate, embryo cell is cut off. Walls are said to appear in this "cell" and so reduce it to a tissue of uninucleate cells. This account certainly does not apply to all species and requires confirmation.

In one or two species the lower half of the sac forms a firm endosperm tissue *before* fertilization, as first observed by J. P. Lotsy in 1899. The accuracy of this observation was questioned by J. M. Coulter in 1908, but it is probable that his preparations did not include the critical stages necessary for confirming or refuting Lotsy's statements, as the latter have since been shown by H. H. W. Pearson to be correct. Coulter described a remarkable development of nutritive tissue, which he named pavement tissue, below the embryo-sac (which is also seen in one or two conifers), and concluded that this had been mistaken by Lotsy for tissue *inside* the embryo-sac.

The later development of the embryo is similar to that of *Welwitschia*, and in both genera a rod-like outgrowth is formed from the hypocotyl at its junction with the radicle, which serves as a feeder and draws nourishment from the endosperm during the germination of the seed.

The climbing species of *Gnetum* are characterized by the production of several concentric cylinders of wood and bast from as many successively formed cambium cylinders produced in the pericycle, as in *Cycas*.

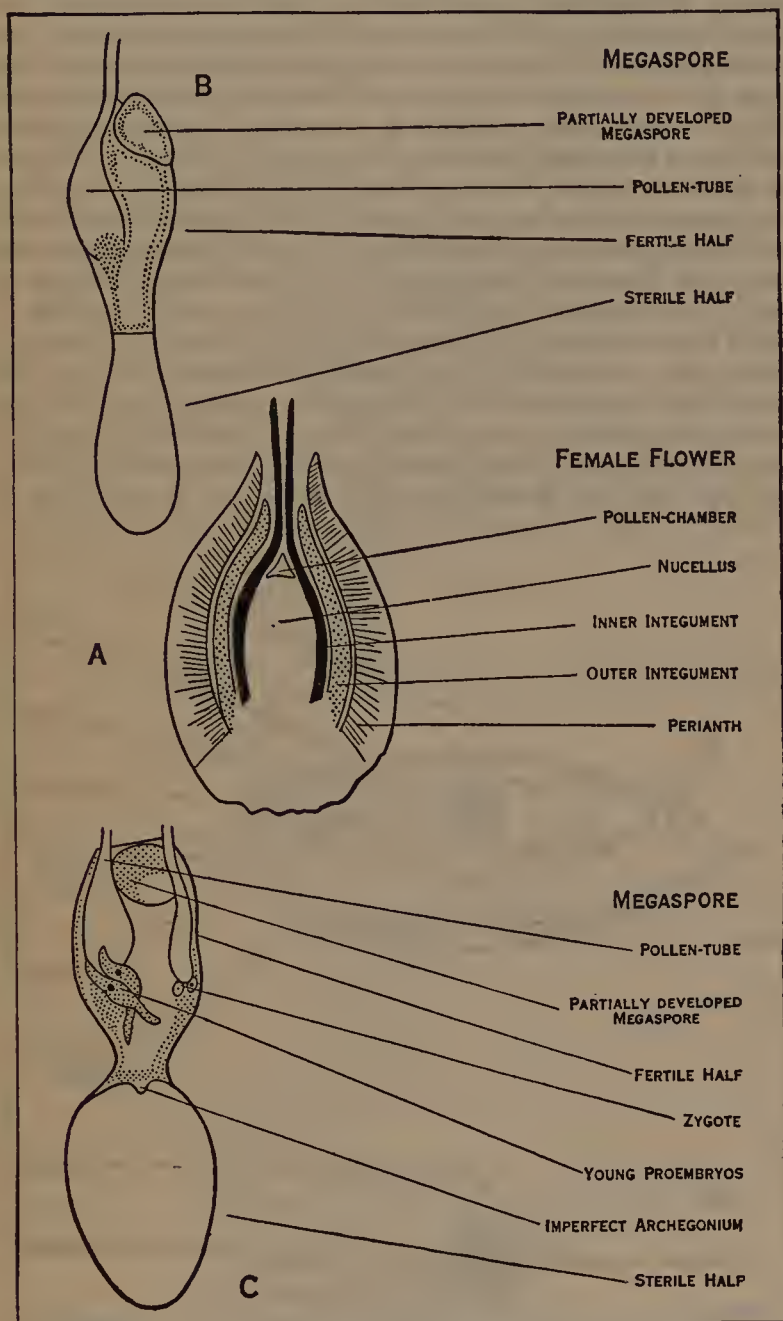
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**CATAPHYLL**, a botanical term for the early leaf-forms produced in the lower part of a shoot, such as bud-scales, or scales on underground stems.

**COLLETER**, a botanical term for the gum-secreting hairs on the buds of certain plants.

**CONIFERS** or **CONIFERALES**: *see* GYMNOSPERMS.

**CULTIGEN**, the horticultural term applied to a plant species or form which does not exist in the wild state. Either spontaneous divergence under cultivation or more direct human agency may have brought about the differentiation from more or less related species or forms in nature. The coco-nut, date and sugar cane are examples. (*See* INDIGEN.)



AFTER LOTSY IN THE "ANNALES DU JARDIN BOTANIQUE DE BINTENZORG" (E. J. BRILL)

FIG. 23.—*GNETUM GNEMON*. A. LONGITUDINAL SECTION OF FEMALE FLOWER; B. PROTHALLUS AT TIME OF FERTILIZATION; C. PROTHALLUS AFTER FERTILIZATION

slender axis projecting above the perianth and terminating in two sporangia. The pollen appears to be formed in precisely the same manner as that of *Welwitschia*. Incomplete female flowers are often found in the male inflorescence containing ovules with one integument instead of two, but these rarely set seed. A perfect female flower (fig. 23) consists of an ovule with three investments of which the outer is generally regarded as a perianth of two concrescent bracts. Of the other two the inner arises first and develops the long slender micropylar tube characteristic of all Gnetales and is followed by a much shorter outer covering, the outer integument. Several megaspores may begin to develop in a young ovule, but only one attains full size. In all species the embryo-sac, as in *Welwitschia*, becomes filled with numerous free nuclei, and in some species, probably in the large majority, fertilization occurs at this stage, the contents of pollen tubes being discharged into the embryo-sac, any of the nuclei near the micropylar end apparently functioning as eggs. The lower half of the sac then becomes partitioned (as in *Welwitschia*) into multi-



**CYME**, the name given in botany to an arrangement of flowers (inflorescence) in which each successive branch of the flowering axis ends in a flower after bearing one or more bracteoles in whose axils the branching is continuous. Cymes are subdivided according to the number of these branches. (See FLOWER.)

**CYSTOLITH**, a botanical term for the inorganic concretions, usually of calcium carbonate, formed in a cellulose matrix in special cells, generally in the leaf of plants of certain families, e.g., *Ficus elastica*, the india-rubber plant.

**CYTOLOGY OF PLANTS:** see, in addition to general article CYTOLOGY, the section *Plant Cytology* of PLANTS.

**YEAST.** The botanist and microbiologist apply the term yeast to a group of plants many of which exhibit a marked ability to change sugar into alcohol and carbon dioxide. The characteristics of the group, which includes hundreds of species, are quite restricted. These, together with discussion of taxonomy, are given under FUNGI and FERMENTATION. To the layman, untrained in botany, the term yeast suggests the cakes of pressed yeast available in almost every hamlet. The ability of certain yeasts to form carbon dioxide from sugar has caused some of them to be used for leavening bread. For centuries, other species have been used in the making of wine, alcohol, beer, etc.

Yeasts probably have as early origin as the bacteria. Grüss examined some fossil remains of Devonian plants and obtained striking evidence of the existence of budding fungi in this early age. This same investigator on examination of the sediment from a beer jar in a Theban tomb of the XIth dynasty (2000 B.C.) isolated a yeast which was named *Saccharomyces Winlocki*. Examination of "beer bread" found among the offerings in other tombs also yielded the same yeast. It is now known that yeasts are widely distributed in nature and that those species concerned in fermentation pass the winter in the soil. They are disseminated by bees, dust and other agents in the spring.

The use of yeast in such fermentations as that of bread has made it convenient to have a constant supply of fresh active yeast. While in former days the by-product of certain fermentation industries was used, pressed (or compressed) yeast is now available to those who desire it. To this end the organism is grown in suitable media and the crop harvested when a sufficient crop of cells has appeared. The medium, according to an older method, consists of wort prepared from grains mashed in water. The mash prepared from grains is inoculated with lactic acid bacteria to "sour" it; the acid prevents putrefaction and also serves as food for the yeasts. The clear wort is passed into fermenters where it receives the seed yeast. The temperature is kept constant and rapid growth takes place. The yeast cells are then separated from the fluid in which they have grown by filter presses. They are mixed with starch and pressed into large cakes. These are sent to distributing centres, where they are cut and wrapped in the small size package commonly used in the home. In more recent times, yeast has been cultivated in mineral salt-sugar solutions instead of the wort described above. The cells are also incorporated in corn meal which is pressed into cakes.

Besides the application of yeasts in fermentology, they have been widely heralded as therapeutic agents. Their application to the cure of disease goes back to very early times. Many of the statements on the use of yeasts in this manner rest upon uncontrolled experiments, if indeed they may be called experiments. We are told that the monks used yeast for curing plague and that Hippocrates advised its use in leucorrhea. Since 1917 great interest was aroused by a publication of Hawk, et al. who reported beneficial results in furunculosis, acne vulgaris, constipation and certain other gastro-intestinal and cutaneous diseases.

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**ANGIOSPERMS.** The botanical term angiosperm (ἀγγεῖον, receptacle, and σπέρμα, seed) was coined in the form Angiospermae by Paul Hermann in 1690, as the name of that one of his primary divisions of the plant kingdom which included flowering

plants possessing seeds enclosed in capsules, in contradistinction to his Gymnospermae, or flowering plants with fruits containing only one seed or dividing into distinct one-seeded portions—the whole fruit or each of its pieces being here regarded as a naked seed. These terms were maintained by Linnaeus with the same sense, but with restricted application, in the names of the orders of his class Didynamia. Their use with any approach to their modern scope only became possible after Robert Brown had established in 1827 the existence of truly naked seeds in the cycads and conifers, entitling them to be correctly called gymnosperms. From that time onwards, so long as these gymnosperms were, as was usual, reckoned as dicotyledonous flowering plants, the term angiosperm was used antithetically by botanical writers, but with varying limitation, as a group-name for other dicotyledonous plants. Wilhelm Hofmeister's brilliant discovery in 1851 of the changes occurring in the embryo-sac of flowering plants, and his determination of the correct relationships of these with the cryptogams (non-flowering plants), fixed the true position of gymnosperms as a class distinct from Dicotyledons, and the term angiosperm then gradually came to be accepted as the suitable designation for the whole of the flowering plants other than gymnosperms, and as including, therefore, the classes of Dicotyledons and Monocotyledons. This is the sense in which the term is used in this article.

The trend of the evolution of the plant kingdom has been in the direction of the establishment of a vegetation of fixed habit and adapted to the vicissitudes of a life on land, and the angiosperms are the highest expression of this evolution and constitute the dominant vegetation of the earth's surface at the present epoch. There is no land-area, from the poles to the equator, where plant-life is possible, upon which angiosperms are not found. They occur also abundantly in the shallows of rivers and fresh-water lakes, and in less numbers in salt lakes and in the sea; such aquatic angiosperms are not, however, primitive forms, but are derived from immediate land-ancestors. Associated with this diversity of habitat is great variety in general form and manner of growth. The familiar duckweed which covers the surface of a pond consists of a tiny green thalloid shoot, one, that is, which shows no distinction of parts—stem and leaf, and a simple root growing vertically downwards into the water. The great forest-tree has a shoot, which in the course perhaps of hundreds of years, has developed a wide-spreading system of trunk and branches, bearing on the ultimate twigs or branchlets innumerable leaves, while beneath the soil a widely-branching root-system covers an area of corresponding extent. Between these two extremes is every conceivable gradation, embracing aquatic and terrestrial herbs, creeping, erect, or climbing in habit, shrubs and trees, and representing a much greater variety than is to be found in the other subdivision of seed-plants, the gymnosperms.

**Internal Structure.**—In internal structure also the variety of tissue-formation far exceeds that found in gymnosperms (see PLANTS: *Anatomy*). The vascular bundles of the stem belong to the collateral type, that is to say, the elements of the wood or xylem and the blast or phloem stand side by side on the same radius. In the larger of the two great groups into which the angiosperms are divided, the Dicotyledons, the bundles in the very young stems are arranged in an open ring, separating a central pith from an outer cortex. In each bundle, separating the xylem and phloem, is a layer of meristem or active formative tissue, known as cambium; by the formation of a layer of cambium between the bundles (interfascicular cambium) a complete ring is formed, and a regular periodical increase in thickness results

**PUBLISHERS' NOTE.**—The articles in this booklet are all taken *verbatim* from the New 14th Edition of the Encyclopaedia Britannica except that material not essential to the subject has been omitted and in a few unimportant instances certain material has been condensed for mechanical reasons. The plates, too, are reproduced unchanged, but the numbering is not always consecutive because the original numbering has been retained in order to agree with the text. A number of cross references to articles not in this booklet have also been retained for the benefit of those who possess the Britannica.



from it by the development of xylem on the inside and phloem on the outside. The soft phloem soon becomes crushed, but the hard wood persists and forms the great bulk of the stem and branches of the woody perennial. Owing to differences in the character of the elements produced at the beginning and end of the season, the wood is marked out in transverse section into concentric rings, one for each season of growth—the so-called annual rings. In the smaller group, the Monocotyledons, the bundles are more numerous in the young stem and scattered through the ground tissue. Moreover, they contain no cambium and the stem once formed increases in diameter only in exceptional cases.

**Vegetative Organs.**—As in the gymnosperms, branching is monopodial, that is, a branch is always developed below the apex of the growing point of the stem or root, dichotomy, or the forking of the growing point into two equivalent branches which replace the main stem, is absent both in the case of the stem and the root. The leaves show a remarkable variety in form (*see* LEAF), but are generally small in comparison with the size of the plant; exceptions occur in some Monocotyledons, *e.g.*, in the Aroid family, where, in some genera the plant produces one huge, much-branched leaf each season, or in palms, where the unbranched stem bears a crown of large leaves.

In rare cases the main axis is unbranched and ends in a flower, as, for instance, in the tulip, where scale-leaves, forming the underground bulb, green foliage-leaves and coloured floral leaves are borne on one and the same axis. Generally, flowers are formed only on shoots of a higher order, often only on the ultimate branches of a much branched system. A potential branch or bud, either foliage or flower, is formed in the axil of each leaf; sometimes more than one bud arises, as for instance in the walnut, where two or three stand in vertical series above each leaf. Many of the buds remain dormant, or are called to development under exceptional circumstances, such as the destruction of existing branches. For instance, the clipping of a hedge or the lopping of a tree will cause to develop numerous buds which may have been dormant for years. Leaf-buds occasionally arise from the roots, when they are called adventitious; this occurs in many fruit trees, poplars, elms and others. For instance, the young shoots seen springing from the ground around an elm are not seedlings but root-shoots. Frequently, as in many Dicotyledons, the primary root, the original root of the seedling, persists throughout the life of the plant, forming, as often in biennials, a thickened tap-root, as in carrot, or in perennials, a much-branched root-system. In many Dicotyledons and most Monocotyledons, the primary root soon perishes and its place is taken by adventitious roots developed from the stem.

**Flower.**—The most characteristic feature of the angiosperm is the flower, which shows remarkable variety in form and elaboration and supplies the most trustworthy characters for the distinction of the orders and families into which the group is divided. The flower is a shoot (a stem bearing leaves) with a special form associated with the special function of ensuring the fertilization of the egg and the development of fruit containing seed. Except where it is terminal it arises, like the leaf-shoot, in the axil of a leaf, which is then known as a bract. Occasionally, as in the violet, a flower arises singly in the axil of an ordinary foliage-leaf; it is then termed axillary. Generally, however, the flower-bearing portion of the plant is sharply distinguished from the foliage-leaf-bearing or vegetative portion and forms a more or less elaborate branch-system in which the bracts are small and scale-like. Such a branch-system is called an inflorescence. The primary function of the flower is to bear the spores (minute one-celled reproductive organs). These, as in gymnosperms, are of two kinds, microspores or pollen-grains, borne in the stamens (or microsporophylls) and megaspores, in which the egg-cell is developed, contained in the ovule, which is borne enclosed in the carpel (or megasporophyll). The flower may consist only of spore-bearing leaves, as in the willow, where each flower comprises only a few stamens or two carpels. Usually, however, other leaves are present which are only indirectly concerned with the reproductive process, acting as protective organs for the sporophylls or forming an attractive envelope. These form the perianth and are in

one series, when the flower is termed monochlamydeous, or in two series (dichlamydeous). In the second case the outer series (calyx of sepals) is generally green and leaf-like, its function being to protect the rest of the flower, especially in the bud; while the inner series (corolla of petals) is generally white or brightly coloured, and more delicate in structure, its function being to attract the particular insect or bird by agency of which transference of pollen (pollination) is effected. The insect, or bird, is attracted by the colour and scent of the flower, and frequently also by nectar which is secreted in some part of the flower. (For further details on the form and arrangement of the flower and its parts, *see* FLOWER.)

**Stamen and Pollen.**—Each stamen generally bears four pollen-sacs (microsporangia) which are associated to form the anther and carried up on a stalk or filament. The development of the microsporangia and the contained spores (pollen-grains) is closely comparable with that of the microsporangia in gymnosperms or heterosporous ferns. The pollen is set free by the opening (dehiscence) of the anther, generally by means of longitudinal slits, but sometimes by pores, as in the heath family (*Ericaceae*), or by valves, as in the barberry. It is then dropped or carried by some external agent, wind, water, or some member of the animal kingdom, on to the receptive surface of the carpel of the same or another flower. The carpel, or aggregate of carpels forming the pistil or gynaecium, comprises an ovary containing one or more ovules and a receptive surface or stigma; the stigma is sometimes carried up on a style. The mature pollen-grain is, like other spores, a single cell; except in the case of some submerged aquatic plants, it has a double wall, a thin delicate wall of unaltered cellulose, the endospore or intine, and a tough outer cuticularized exospore or extine. The exospore often bears spines or warts, or is variously sculptured, and the character of the markings is often of value for the distinction of genera or higher groups. Germination of the microspore begins before it leaves the pollen-sac. In very few cases has anything representing the development of tissue, comparable with the prothallium of a fern, been observed; generally a small cell (the antheridial or generative cell) is cut off, leaving a larger tube-cell. When placed on the stigma, under favourable circumstances, the pollen-grain puts forth a pollen-tube which grows down the tissue of the style to the ovary, and makes its way along the placenta, guided by projections or hairs, to the mouth of an ovule. The nucleus of the tube-cell has meanwhile passed into the tube, as does also the generative nucleus which divides to form two male or sperm-cells. The male cells are carried to their destination in the tip of the pollen-tube.

**Pistil and Embryo-Sac.**—The ovary contains one or more ovules borne on a placenta, which is generally some part of the ovary-wall. The development of the ovule, which represents the macrosporangium, is very similar to the process in gymnosperms; when mature it consists of one or two coats surrounding the central nucellus; except at the apex where an opening, the micropyle, is left. The nucellus is a cellular tissue enveloping one large cell, the embryo-sac or macrospore. The germination of the macrospore consists in the repeated division of its nucleus to form two groups of four, one group at each end of the embryo-sac. One nucleus from each group, the polar nucleus, passes to the centre of the sac, where the two fuse to form the endosperm nucleus. Of the three cells at the micropylar end of the sac, all naked cells (the so-called egg-apparatus), one is the egg-cell or oosphere, the other two, which may be regarded as representing abortive egg-cells (in rare cases capable of fertilization), are known as synergidae. The three cells at the opposite end are known as antipodal cells and become invested with a cell-wall. The gametophyte or prothallial generation is thus extremely reduced, consisting of but little more than the male and female sexual cells—the two sperm-cells in the pollen-tube and the egg-cell (with the synergidae) in the embryo-sac.

**Fertilization.**—At the period of fertilization the embryo-sac lies in close proximity to the opening of the micropyle, into which the pollen-tube has penetrated, the separating cell-wall becomes absorbed, and the male or sperm-cells are ejected into the embryo-sac. Guided by the synergidae one male-cell passes into the oosphere with which it fuses, the two nuclei uniting, while the other



fuses with the endosperm-nucleus. After impregnation the fertilized oosphere immediately surrounds itself with a cell-wall and becomes the oospore, which by a process of growth forms the embryo of the new plant. The endosperm-nucleus divides rapidly to produce a cellular tissue which fills up the interior of the rapidly growing embryo-sac, and forms a tissue, endosperm, in which is stored a supply of nourishment for the use later on of the embryo.

We can recognize, therefore, two products of fertilization—one, the embryo, which becomes the future plant; the other, the endosperm, a short-lived undifferentiated nurse to assist in the nutrition of the former. The endosperm, like the embryo, being the product of a sexual act, hybridization will give a hybrid endosperm as it does a hybrid embryo, and herein we may have the explanation of the phenomenon of “xenia” observed in the mixed endosperms of hybrid races of maize and other plants. The antipodal cells aid more or less in the process of nutrition of the developing embryo, and may undergo multiplication, though they ultimately disintegrate, as do also the synergidae. As in gymnosperms and other groups an interesting qualitative change is associated with the process of fertilization. The number of chromosomes (*see* CYTOLOGY) in the nucleus of the two spores, pollen-grain and embryo-sac is only half the number found in an ordinary vegetative nucleus, and this reduced number persists in the cells derived from them. The full number is restored in the fusion of the male and female nuclei in the process of fertilization and remains until the formation of the cells from which the spores are derived in the new generation.

The above is a general account representing the normal sequence of events, but various departures have been noted. Thus in the family Rosaceae, the order Fagales and the anomalous genus *Casuarina* and others, instead of a single macrspore a sporogenous tissue is formed, but only one cell proceeds to the formation of a functional female cell. In *Casuarina*, *Juglans* and the family Corylaceae, the pollen-tube does not enter by means of the micropyle, but, passing down the ovary-wall and through the placenta, enters at the opposite, or chalazal, end of the ovule. Such a method of entrance is styled chalazogamic, in contrast to the porogamic or ordinary method of approach by means of the micropyle.

**Embryology.**—The result of fertilization is the development of the ovule into the seed. By the segmentation of the fertilized egg, invested by cell-membrane, the embryo plant arises. A varying number of transverse segment-walls transform it into a pro-embryo—a cellular row of which the cell nearest the micropyle becomes attached to the apex of the embryo-sac, and thus fixes the position of the developing embryo, while the terminal cell is projected into its cavity. In Dicotyledons the shoot of the embryo is wholly derived from the terminal cell of the pro-embryo, from the next cell the root arises, and the remaining ones form the suspensor. In many Monocotyledons the terminal cell forms the cotyledonary portion alone of the shoot of the embryo, its axial part and the root being derived from the adjacent cell; the cotyledon is thus a terminal structure and the apex of the primary stem a lateral one—a condition in marked contrast with that of the Dicotyledons. In some Monocotyledons, however, the cotyledon is not really terminal. The primary root of the embryo in all angiosperms points towards the micropyle. The developing embryo at the end of the suspensor grows out to a varying extent into the forming endosperm, from which by surface absorption it derives food-material for growth; at the same time the suspensor plays a direct part as a carrier of nutrition, and may even develop, where perhaps no endosperm is formed, special absorptive “suspensor roots” which invest the developing embryo, or pass out into the body and coats of the ovule, or even into the placenta. In some cases the embryo or the embryo-sac sends out suckers into the nucellus and ovular integument. As the embryo develops it may absorb all the food-material available, and store, either in its cotyledons or in its hypocotyl (the short portion of the stem below the cotyledons), what is not immediately required for growth, as reserve-food for use in germination, and by so doing it increases in size until it may fill entirely the embryo-sac; or its absorptive power at this stage may be limited to what is necessary for growth

and it remains of relatively small size, occupying but a small area of the embryo-sac, which is otherwise filled with endosperm in which the reserve-food is stored. There are also intermediate states. The position of the embryo in relation to the endosperm varies; sometimes it is internal, sometimes external, but the significance of this has not yet been established.

The formation of endosperm starts, as has been stated, from the endosperm-nucleus. Its segmentation always begins before that of the egg, and thus there is timely preparation for the nursing of the young embryo. If in its extension to contain the new formations within it the embryo-sac remains narrow, endosperm formation proceeds upon the lines of a cell-division; but in wide embryo-sac the endosperm is first of all formed as a layer of naked cells around the wall of the sac and only gradually acquires a pluricellular character, forming a tissue filling the sac. The function of the endosperm is primarily that of nourishing the embryo, and its basal position in the embryo-sac places it favourably for the absorption of food material entering the ovule. Its duration varies with the precocity of the embryo. It may be wholly absorbed by the progressive growth of the embryo within the embryo-sac, or it may persist as a definite and more or less conspicuous constituent of the seed. When it persists as a massive element of the seed its nutritive function is usually apparent, for there is accumulated within its cells reserve-food, and according to the dominant substance it is starchy, oily, or rich in cellulose, mucilage, or proteid. In cases where the embryo has stored reserve-food within itself and thus provided for self-nutrition, such endosperm as remains in the seed may take on other functions, for instance, that of water-absorption.

Some deviations from the usual course of development may be noted. Parthenogenesis, or the development of an embryo from an egg-cell without the latter having been fertilized, has been described in species of *Thalictrum*, *Antennaria*, and *Alchemilla*. Polyembryony is generally associated with the development of cells other than the egg-cell. Thus in *Erythronium* and *Limnorcharis* the fertilized egg may form a mass of tissue on which several embryos are produced. Isolated cases show that any of the cells within the embryo-sac may exceptionally form an embryo, *e.g.*, the synergidae in species of *Mimosa*, *Iris*, and *Allium*, and in the last-mentioned the antipodal cells also. In *Coelebogynne* (Euphorbiaceae) and in *Funkia* (Liliaceae) polyembryony results from an adventitious production of embryos from the cells of the nucellus around the top of the embryo-sac. In a species of *Allium* embryos have been found developing in the same individual from the egg-cell, synergids, antipodal cells, and cells of the nucellus. In two Malayan species of *Balanophora* the embryo is developed from a cell of the endosperm, which is formed from the upper polar nucleus only, the egg-apparatus becoming disorganized. The last-mentioned case has been regarded as representing an apogamous development of the sporophyte from the gametophyte comparable to the cases of apogamy described in ferns. But the great diversity of these abnormal cases as shown in the examples cited above suggests the use of much caution in formulating definite morphological theories upon them.

As the development of embryo and endosperm proceeds within the embryo-sac its wall enlarges and commonly absorbs the substance of the nucellus (which is likewise enlarging) to near its outer limit, and combines with it and the integument to form the seed-coat; or the whole nucellus and even the integument may be absorbed. In some plants the nucellus is not thus absorbed, but itself becomes a seat of deposit of reserve-food constituting the perisperm which may coexist with endosperm, as in the water-lily family (Nymphaeaceae), or may alone form a food-reserve for the embryo, as in *Canna*. Endospermic food-reserve has evident advantages over perispermic, and the latter is comparatively rarely found. Seeds in which endosperm or perisperm, or both, exist are commonly called albuminous or endospermic; those in which neither is found are termed exalbuminous or ex-endospermic. The presence or absence of endosperm, its relative amount when present, and the position of the embryo within it are valuable characters for the distinction of families and orders, or groups of families. Meanwhile the ovary-wall has developed to



form the fruit or pericarp, the structure of which is closely associated with the manner of distribution of the seed. Frequently the influence of fertilization is felt beyond the ovary, and other parts of the flower take part in the formation of the fruit, as the floral receptacle in the apple, strawberry, and others. The character of the seed-coat bears a definite relation to that of the fruit. Its function is the twofold one of protecting the embryo and of aiding in dissemination; it may also directly promote germination. If the fruit is a dehiscent one and the seed is, therefore, soon exposed, the seed-coat has to provide for the protection of the embryo and may also have to secure dissemination. On the other hand, indehiscent fruits discharge these functions for the embryo, and the seed-coat is only slightly developed.

**Dissemination.**—Dissemination is effected by an explosive mechanism resident in the fruit or seed, or by aid of some external agency—water, air, or animals. The need for this is obvious—buoyancy in water and resistance to wetting for the first, some sort of parachute for the second, and some attaching mechanism or attractive structure for the third. The methods in which these are provided are of infinite variety, and any and every part of the flower and of the inflorescence may be called into requisition to supply the adaptation (*see* FRUIT). Special outgrowths, arils, of the seed-coat are of frequent occurrence. In the feature of the fruit and seed, by which the distribution of angiosperms is effected, we have a distinctive character of class. In gymnosperms we have seeds, and the carpels may become modified and close around these, as in *Pinus* during the process of ripening to form an imitation of a box-like fruit which, subsequently opening, allows the seeds to escape; but there is never in them the closed ovary investing from the outset the ovules and ultimately forming the groundwork of the fruit.

**Germination of Seed.**—Their fortuitous dissemination does not always bring seeds upon a suitable nidus for germination, the first need for which is a sufficiency of moisture, and the duration of vitality of the embryo is a point of interest. Some seeds retain vitality for a period of many years, though there is no warrant for the popular notion that genuine “mummy wheat” will germinate; on the other hand some seeds lose vitality in a very short time. Further, the older the seed the more slow as a general rule will germination be in starting; but there are notable exceptions. This pause, often of so long duration, in the growth of the embryo between the time of its perfect development within the seed and the moment of germination, is one of the remarkable and distinctive features of the life of seed-plants (spermatophytes). The aim of germination is the fixing of the embryo in the soil, effected usually by means of the root, which is the first part of the embryo to appear, in preparation for the elongation of the portion of the shoot above the cotyledons (*epicotyl*), and there is infinite variety in the details of the process. In endospermic Dicotyledons the cotyledons act as the absorbents of the reserve-food of the seed and are commonly brought above ground (*epigeal*), either withdrawn from the seed-coat or carrying it upon them, and then they serve as the first green organs of the plant. The part of the stem below the cotyledons (hypocotyl) commonly plays the greater part in bringing this about. Exendospermic Dicotyledons usually store reserve-food in their cotyledons, which may in germination remain below ground (*hypogeal*). In endospermic Monocotyledons the cotyledon itself, probably in consequence of its terminal position, is commonly the agent by which the embryo is thrust out of the seed, and it may function solely as a feeder, its extremity developing as a sucker through which the endosperm is absorbed, or it may become the first green organ, the terminal sucker dropping off with the seed-coat when the endosperm is exhausted. Exendospermic Monocotyledons are either hydrophytes or strongly hygrophilous plants and have often peculiar features in germination.

**Vegetative Reproduction.**—Distribution by seed appears to satisfy so well the requirements of angiosperms that distribution by vegetative buds is only an occasional process. At the same time every bud on a shoot has the capacity to form a new plant if placed in suitable conditions, as the horticultural practice of propagation by cuttings shows; in nature we see plants spreading

by the rooting of their shoots, and buds we know may be freely formed not only on stems but on leaves and on roots. Where detachable buds are produced, which can be transported through the air to a distance, each of them is an incipient shoot which may have a root, and there is always reserve-food stored in some part of it. In essentials such a bud resembles a seed. A relation between such vegetative distribution buds and production of flower is usually marked. Where there is free formation of buds there is little flower and commonly no seed, and the converse is also the case. Viviparous plants are an illustration of substitution of vegetative buds for flower. In these cases the ovule is replaced by a minute plantlet which develops *in situ* and separates from the plant when it is able to maintain an independent existence. This occurs in some grasses and other species living in Arctic or other situations where the normal course of seed-development as the result of fertilization is uncertain.

**Phylogeny and Taxonomy.**—Reference is made in the general article BOTANY to early systems of classification and to the evolution of the idea of a natural system in which families were grouped according to their affinities. This found expression in British botany in the system elaborated by George Bentham and Joseph Hooker in the *Genera Plantarum* (1862–1883), in which all known genera of flowering plants were described and arranged in families and higher groups. The system was based on that of the De Candolles and has been widely used in Great Britain and America. It will illustrate the principles of a system which, without claiming to be phylogenetic, represents in the sequence adopted a progression from simpler to more advanced families. The families of the two great divisions, Dicotyledons and Monocotyledons, are grouped in cohorts (or series); those of the Dicotyledons are arranged in three subdivisions: Polypetalae, where the petals are free from each other, Gamopetalae, with a corolla of united petals, and Monchlamydeae, without a corolla, and where the flower often consists merely of the reproductive organs. (*See* the article FLOWER for illustrations.) In the first two subdivisions the cohorts are arranged in a progressive series according to the relative position of the gynaecium and the other floral whorls; in the simplest forms sepals, petals, and stamens stand below the carpels on the floral axis (*i.e.*, are hypogynous), while in the most advanced they spring from the top of the ovary (*i.e.*, are epigynous). Diminution of the number of parts in the flower is also an indication of an advance, especially the number of carpels which in the most advanced members of each subdivision is reduced to two. A spiral arrangement of the floral leaves is also more primitive than a whorl; and a regular flower, that is one showing a radial structure, than one which is symmetrical only about one plane. To some extent also a woody habit indicates less advance than an herbaceous.

A great drawback to the value of this system is the inclusion among the Monochlamydeae of a number of families which are closely allied with families of Polypetalae though differing in absence of a corolla. The German systematist, A. W. Eichler, attempted to remove this disadvantage which since the time of Jussieu had characterized the French system, and in 1883 grouped the Dicotyledons in two subclasses. The earlier subclass, Chori-petalae, embraces the Polypetalae and Monochlamydeae of the French and English systems, and is an attempt to arrange as far as possible in a linear series those families which are characterized by absence or freedom of petals. A modification of Eichler's system, embracing more recent views of the affinities of the families of angiosperms, has been put forward by Dr. Adolf Engler of Berlin, who adopts the suggestive names Archichlamydeae and Metachlamydeae for the two subdivisions of Dicotyledons. Engler regarded his system as phylogenetic; simplicity of floral structure was considered primitive and the earlier orders (as groups of families are now termed) in his system are thus characterized. But he recognized that a simple type of flower may also appear in an advanced group and is then obviously derived; and many botanists would regard all families characterized by simple flowers as derived from more advanced forms.

Divergent views as to the origin of the angiosperms have some bearing on this problem. The angiosperms appear in the Creta-



ceous period as a well-developed and widely distributed group of plants with the characters of the existing class. The fossil remains may be distributed among existing families and genera and give no clue to the early history of the group.

The great antiquity of the other class of seed-plants, the gymnosperms, has suggested that the origin of the angiosperms should be sought within it. Thus Richard Wettstein seeks to derive a simple form of flower from an ancestor, resembling *Ephedra* (Gnetaceae), and regards the simple flower as primitive in the angiosperms. A view which has found considerable support regards the extinct Mesozoic Cycadeoidea, a group allied to the cycads, as the nearest approach known to the ancestral angiosperm stock. The "flower" of Bennettites (see PALAEOBOTANY), which has an elongated axis bearing sterile leaves below and micro- and macro-sporophylls above, is regarded as the forerunner of the angiosperm flower as exhibited, for instance, in *Magnolia*, a perfect bisexual flower with free sepals, petals, stamens, and carpels following in spiral succession on an elongated floral receptacle. On this theory, which has been developed by E. A. N. Arber and J. W. Parkin (see *Journ. Linn. Soc. [Bot.]* xxxviii. 29, 1907), this type of flower represents the starting point of a phylogenetic system of classification of Dicotyledons. Such are the systems elaborated by C. E. Bessey in America, Hans Hallier in Germany, and recently by John Hutchinson in England.

It is, however, probable that the original stock of the angiosperms has not yet been traced. A vast number of forms must have arisen and become extinct in the course of evolution of the group, and among these may be some of which certain of the existing simple-flowered groups are surviving representatives.

The relation of the two divisions, Dicotyledons and Monocotyledons, has also been much debated. Had each group a separate origin or has one been derived from the other? Botanists who uphold the Bennettites ancestry of Dicotyledons would derive the Monocotyledons from the base of the dicotyledonous stock. But strong arguments have been adduced in favour of its distinct origin, the two divisions representing a parallel development.

A phylogenetic tree including the whole plant-kingdom has recently been elaborated by Carl Mez and H. Ziegenspeck, based on the reaction to serum of members of the various families (see Von C. Mez and H. Ziegenspeck, "Der Königsberger Serodiagnostische Stammbaum," *Mez, Botanisches Archiv*. xiii. 482 [1926]).

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**HIBERNACULUM**, in botany a term for a winter bud; in botanical gardens, the winter quarters for plants.

**HONEY DEW**, a secretion consisting of exudations of sugar from the leaves of various trees under certain atmospheric conditions. It is usually the result of a superfluity of sap, but may also be produced by the puncture of certain insects (*Aphides*, *q.v.*); the latter condition constitutes a form of plant disease. See PLANTS: Pathology.

**UMBEL**, in botany, an inflorescence in which the stalks of the flowers all spring from the top of the main stalk, thus usually producing a flat-topped flower head, as in the carrot, parsnip and fennel. (See FLOWER.)

**MYCORRHIZA**. The roots of land plants live in soil, competing therein for water and nutrients with a crowded population of micro-organisms. They are surrounded by a rich and varied fungus flora many members of which are potential parasites, but

the majority of roots are relatively immune to such parasitic attack and continue to flourish side by side with their fungus competitors. To the interaction of these three phenomena—the competitive struggle for food, the capacity of many fungi to penetrate living tissues and the properties of resistance to such invasion possessed by roots in common with organisms in general—is probably due the evolution of *mycorrhiza*, that curious and interesting partnership between the roots of vascular plants and fungus mycelium now known to affect a vast number of the higher plants and to be of great importance in their lives.

Mycorrhizae or fungus-roots (μύκης, a mushroom) (ρίζα, a root) are formed alike by wild and cultivated plants, by species from the high mountains and by those from salt marshes at sea level, in the vegetation of tropical forests as in that within the arctic circle. The phenomenon was comparatively well-known, especially to foresters when, in 1885, the German botanist, Frank, coined the new name, 'mycorrhiza,' to register his own view that the root with its associated mycelium constituted an independent organ of great importance in plant nutrition. He reported an invariable and intimate association of fungus mycelium with the roots of forest trees, especially oak, beech, hornbeam and other members of Cupuliferae, and certain conifers, such infection being, in his opinion, not parasitic but of definite service to the trees in relation to the absorption of water and nutrient salts. On a contemporary view associated especially with the name of Robert Hartig, the root fungi of trees were mischievous parasites hindering root action and conferring no benefit upon the hosts.

By the end of the nineteenth century it was realized by botanists that the mycorrhizal habit was widespread, affecting not only trees but an immense number of herbaceous species belonging to different families.

**Distribution and Structure.**—Mycorrhiza is formed by ferns, club mosses, conifers and an ever growing list of flowering plants belonging to many different families. It is constant and conspicuous in certain groups, *e.g.*, Orchidaceae, Ericales, Empetraceae and forest trees generally, and is invariably well developed in species lacking chlorophyll, *e.g.*, *Neottia Nidus-avis*, *Coralorrhiza* spp. and a number of tropical orchids belonging to this class, members of the Monotropoideae, and certain species belonging to the families Gentianaceae and Burmanniaceae. Structures closely resembling the mycorrhizal tissues of living species have been described in fossils of Coal Measure age. It is specially characteristic of the vegetation of humus soils, *viz.*, those of moorlands, woodlands and heaths, but may be well developed in garden soil and in the most diverse situations elsewhere. It may be regarded as an annual phenomenon affecting all or a proportion only of the young absorbing roots of the current year.

It is assumed that the fungi concerned are widely distributed in soil, and with few exceptions invasion of the roots takes place from this source. The effect of infection is strikingly different from that in ordinary parasitism, there being no indication that the tissues suffer any permanent injury from the more or less extensive infestation by mycelium to which they are subjected. The external appearance of the root may be altered, as in trees, where arrest of growth accompanied by profuse branching results in the production of dense clusters of rootlets, brown or variously coloured according to the kind of mycelium present. Sometimes the appearance of the roots is not altered in any way. There is great variation in different plants and at different seasons in respect to the relative abundance of mycelium, its distribution upon and within roots and the details of structure of individual mycorrhizas.

It is still convenient to recognize two main types of structure and use the descriptive names given to them by Frank in 1885; the *ectotrophic* type, specially characteristic of trees, in which mycelium completely invests the tip and younger portion of the root as with a sheath of varying thickness, branches from which penetrate between the cortical cells to form a continuous network, while individual cells remain relatively immune from infection; and the *endotrophic* type, showing a variable amount of mycelium externally without formation of a sheath, combined with a more or less profuse distribution of hyphae within the



cells, sometimes irregularly distributed in the cortical tissues, sometimes localized in definite zones. The individual cells that suffer invasion become filled with coiled or branched hyphae continuous with those which form an irregular mesh upon the external surface of the root and permeate the soil around it. In a majority of fungus-roots these intracellular hyphal complexes disintegrate, dwindle and disappear, the soluble by-products presumably passing to the host cells.

These two types of mycorrhiza are not sharply distinguished from one another as Frank believed. It is known now that those of the ectotrophic type often exhibit relatively heavy infection of individual cells, and it seems probable that the structural differences are related to the character of the mycelium and to soil conditions rather than to any fundamental distinction in the association as a whole.

**The Mycorrhiza of Orchids.**—The mycorrhiza of orchids is of the endotrophic type and mycelium may be widely distributed throughout the root cortex or confined to certain regions. Two contrasting types of cell are observable: *Pilzwirthezellen* or "host cells," containing active hyphae, and *Verdauungszellen* or "digestion-cells," enclosing only their disintegrated remains subsequent to digestion. In the former the mycelium fills the cells with skeins or "pelotons" of characteristic appearance and probably abstracts nutrient materials from the host; in the latter these substances and possibly others brought in from the soil are placed at the disposal of the root.

The researches of a French botanist, Bernard, initiated a new method of experimental inquiry and demonstrated the far-reaching character of the relationship in orchids. The difficulties experienced by growers in germinating seeds of orchids had long been known. Bernard isolated the root fungi from a number of species and showed, by "pure culture" methods, that germination of seed and development of the seedling are bound up with infection by the appropriate root fungus at a critical stage of development. In nature, this *symbiotic* type of germination is ensured by the presence of mycelium of the root fungus in the soil about the roots of the parent plant; in horticultural practice, artificial cultures have been successfully utilized by L. Knudson for the same purpose. It has been discovered that the stimulus normally provided by the appropriate fungus can be replaced artificially by carefully adjusting the chemical constitution and reaction of the seedbed, and such *asymbiotic* methods of securing germination have been successfully applied by horticulturalists in the case of certain orchid species.

There remains much that is obscure in the relation of fungus and host in this group of plants. The nature of the problems awaiting solution is sufficiently indicated by the invariable association of particular fungus strains with individual orchid species, and by the fact that orchid growing is concerned not only with the cultivation of natural species but with the raising of new hybrids.

**Mycorrhiza in Ericaceae.**—In northern Europe certain members of the family Ericaceae, e.g., various kinds of heath (*Erica* spp.), and heather or ling (*Calluna vulgaris*) are a constant feature of the vegetation of humus soils—moorland and woodland—on which they often monopolize large areas to the almost complete exclusion of other plants.

Described by Frank as *obligate mycorrhiza plants*, it was early recognized that members of this group might exhibit specialized relations with their root fungi. The mycorrhiza is of the endotrophic type with certain characteristic features, in some respects showing points of resemblance with that of trees. The young roots are excessively fine, the outermost layer of cells in each forming a definite mycorrhizal zone. In favourable soil conditions practically every cell in this layer is filled with a densely branched complex of fungal hyphae from which strands of mycelium extend outwards into the soil. The growth of mycelium on the outside of the roots is rather more profuse than in orchids, and, in certain species, may resemble the sheath-like condition found in ectotrophic mycorrhizas. As in orchids, the complexes of mycelium within the root cells are subject to rapid and complete digestion followed by disappearance of the resulting products.

In ling (*Calluna vulgaris*) and certain allied species an obligate relation unique of its kind has been revealed by experimental research. In these plants the mycelium which infests the root spreads throughout the tissues of the vegetative shoots, flowers and fruits reaching eventually the seed-coats of the developing seeds. These are shed bearing with them the mycelium of the fungus partner and at germination the emerging seedling is immediately subject to invasion.

The distribution of mycelium throughout the plant thus compares sharply with that found in orchids where it is limited to the roots of the adult and the embryonic tissues of the seedling. In *Calluna* and kindred ericaceous species it is practically co-extensive with the plant tissues. Only the embryo and endosperm of the resting seed are free from contamination; at all other stages of development and throughout its vegetative existence every plant of ling yet examined is a dual organism. In the genus *Vaccinium* the intimacy of the relation has been carried a stage farther and mycelium is present, not only externally upon the seed-coats, but internally throughout the tissues of the seed. The mode of infection observed in Ericaceae is unique, for, in all other known cases, the mycelium responsible for forming mycorrhiza enters the root from the soil.

In ling and probably in allied species the formation of functional mycorrhiza is closely related to soil conditions. It is at a maximum in peaty soils and in cultivated soils with abundant humus, much less conspicuous in sandy soils deficient in organic matter, and may appear to be absent under certain conditions, although roots are never free from fungus infection.

Since seedling development follows and depends upon invasion by fungus mycelium at germination, it is impossible to provide experimental evidence bearing on the behaviour of individuals with and without fungus infection.

**The Mycorrhiza of Trees.**—The mycorrhiza of trees is characteristic and easily recognized. Structurally, it belongs to the ectotrophic type; each rootlet is enveloped in a sheath of mycelium formed by the close interweaving of hyphae continuous internally with a branch system penetrating between the cells of the roots, externally with the network of mycelium in the soil.

Woodland soils possess an unusually rich and varied fungus flora among which members of the great group known as Hymenomycetes are conspicuous, as evidenced by the profusion of their spore-bodies—toadstools—produced during suitable seasons. So constant is the association of some of these with certain trees that it has been said that they follow the latter "as the dolphin follows the ship."

In order to prove a direct relation between these common woodland fungi and the mycorrhiza of the trees beneath which they grow, it was necessary to isolate the endophytes, learn something of their behaviour and compare the growth of young trees with and without mycorrhiza. By such means a number of Hymenomycetes have been identified as the specific root fungi of pine, spruce, larch, birch and other trees.

There is no evidence that seedling development is bound up with fungus infection or that anything in the nature of an obligate relation exists. As regards the effect of tree mycorrhiza on nutrition, it must be noted that woodland soils possess certain definite characteristics. There is severe competition for water and salts and they show a notable deficiency of certain plant nutrients, in particular nitrates. On the other hand, they possess large reserves of nitrogen in the form of organic compounds. It has been proved experimentally that the possession of mycorrhiza is beneficial to trees, especially in relation to the supply of nitrogenous nutrients. Hence, the supply of nitrates being deficient it may be concluded that it possesses a vital significance for trees and other plants growing in woodland soils. The application of these conclusions to natural conditions raises problems of great importance to practical foresters.

**Identity of Mycorrhizal Fungi.**—It may be assumed that the fungi responsible for forming mycorrhiza are widely distributed in soil. Their systematic position is known only in those forms which have been isolated and grown in "pure culture" out-



side the root.

The root fungi of orchids are generally recognized as belonging to a common group, sometimes included in the well-known genus *Rhizoctonia*, sometimes placed in a new genus *Orcheomyces*. The mycelium must be locally present about the roots of wild orchids but nothing is known as to its wider distribution.

The mycorrhizal fungi of *Calluna* and other ericaceous species have been isolated and included in a single species of the genus *Phoma*, *P. radialis*. The specialized strains associated with different ericaceous species are distinct and must be locally distributed in heath and moorland soils but there is no certain knowledge of their wider occurrence.

The fungi definitely identified with the mycorrhiza of trees belong to the genera *Boletus*, *Amanita*, *Cortinarius*, *Lactarius*, *Russula* and *Tricholoma*. It is probable that many others will prove to belong to the same category.

Outside these specialized groups, the fungi responsible for mycorrhiza-formation still await identification. The mycelium present in a large number of herbaceous flowering plants, certain ferns and club mosses is uniform in type and produces characteristic structures: round or pear-shaped swellings or *vesicles*, variously regarded as organs relating to spore-formation or to the storage of reserves, and intracellular branch systems first described by Gallaud in 1905 under the name of *arbuscules*. Following upon digestive activity in the host cells the latter disintegrate to structureless masses named *sporangioles* before their true nature is recognized. The fungus responsible for this widespread type of mycorrhiza has hitherto resisted all attempts at isolation and nothing is known with certainty as to its systematic position.

It has been reported that the mycorrhiza of many herbaceous plants is of dual character, involving primary infection by a fungus with the characters just described followed by secondary infection by one of the type associated with orchid roots. Whether this reported "double infection" is of biological significance is at present unknown.

**Rôle of Mycorrhiza in Plant Growth.**—There can be little doubt that the mycorrhizal habit had its origin in parasitic attack on the part of certain soil fungi, or that existing mycorrhiza plants are the survivors of a long and perilous evolutionary history. Many must be regarded as cases of compromise fluctuating between an almost complete resistance to fungus invasion and a remarkable toleration of the same. That there is an exchange of nutrient material in practically all cases can hardly be doubted but, in the absence of information based on the behaviour of individuals with and without mycorrhiza, attempts to express the shifting relationships in terms of mutual advantage or the reverse are premature and often misleading.

In certain groups of plants mycorrhiza has become a regular feature in the life history, a condition of delicately balanced equilibrium between fungus and host has been established and critical experimental study has placed certain facts beyond doubt. In both orchids and heaths the normal development of the seedling is bound up with the presence and activities of mycorrhizal fungi showing marked adaptation to individual species, accompanied in members of Ericaceae by a distribution of mycelium throughout the tissues so extensive that it is difficult to conceive of the individual plant as other than a single entity of double constitution. In orchids, the traditional view attributes a beneficial rôle to the root fungi based on their utilization of organic soil constituents and the wholesale digestion of mycelium that takes place subsequently in the root-cells. A claim has been advanced for fixation of atmospheric nitrogen by the root fungi of several orchid species.

It may be safely concluded that mycorrhiza possesses a vital significance for trees and other plants growing in woodland soils, and there is reason to believe that the reaction and constitution of the soil are important factors in promoting its healthy development and functioning. In the Ericaceae, *Calluna* and many of its allies are characteristic and abundant members of the vegetation of humus soils thus pointing to similar conclusions, while in this group there is likewise evidence that the capacity to draw indirectly upon the organic compounds in the soil humus is sup-

plemented by the ability of the root fungi to utilize atmospheric nitrogen. In both orchids and heaths the obligate character of the association is probably confined to the seedling phase and does not extend to the adult, although in heaths infection of the roots follows directly upon that of the seedling tissues.

The older theories of beneficial symbioses in mycorrhiza were deduced from distribution and structure untested by experiment. Modern research has been marked by the application of new and more precise methods and has revealed unsuspected relationships. On the whole, it supports the view that the possession of mycorrhiza is frequently of service to vascular plants, the nature and degree of benefit depending upon the physical conditions of the environment and the character of the association in individual cases. (M. C. R.)

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**HETEROSPORY**, the name given in botany to the phenomenon of plants producing two kinds of spores.

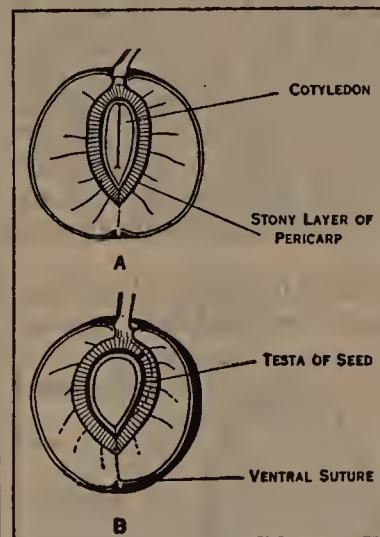
**INDIGEN**, the horticultural term applied to a plant species or form which originated in a natural habitat in distinction from cultigen (*q.v.*), a plant form originated in cultivation.

**MERISTEM**, a botanical term for tissue which has the power of developing new forms of tissue, such as the cambium from which new wood is developed or the tissue at the apex which is responsible for the growth in length of the stem or root.

**ROSACEAE**, in botany, a large cosmopolitan family of seed-bearing plants which belong to the series Rosales of dicotyledons and containing about 100 genera with 2,000 species. The plants vary widely in manner of growth. Many are herbaceous, growing erect, as *Geum*, or with slender creeping stem, as in species of *Potentilla*, sometimes sending out long runners, as in straw-

berry; others are shrubby, as raspberry, often associated with a scrambling habit, as in the brambles and roses, while apple, cherry, pear, plum and other British fruit trees represent the arborescent habit. Vegetative propagation takes place by means of runners, which root at the apex and form a new plant, as in strawberry; by suckers springing from the base of the shoot and rising to form new leafy shoots after running for some distance beneath the soil, as in raspberry; or by shoots produced from the roots, as in cherry or plum. The scrambling of the brambles and roses is effected by means of prickles on the branches and leaf-stalks.

The leaves, which are arranged alternately, are simple, as in apple, cherry, etc., but more often compound, with leaflets pal-



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

**CHERRY (PRUNUS CERASUS)**

A. Vertical section of the drupe of Cherry, cut vertically through the ventral and dorsal suture; B. fruit cut vertically in a plane at right angles to preceding one

mately arranged, as in strawberry and species of *Potentilla*, or pinnately arranged, as in the brambles, roses, mountain ash, etc. A difference in this respect often occurs in one and the same genus, as in *Pyrus*, where apple (*P. Malus*), and pear (*P. communis*) have simple leaves, whereas mountain ash or rowan (*P. aucuparia*) has pinnately compound leaves. In warm climates the leaves are often leathery and evergreen. The leaves are stipulate, the stipules being sometimes small and short-lived, as in *Pyrus* and *Prunus* (cherry, plum, etc.), or more important structures adnate to the base of the leaf-stalk, as in roses, brambles, etc. The flowers,

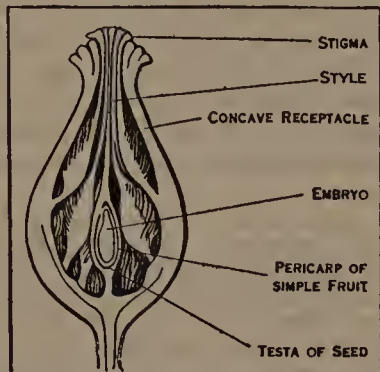


which are regular, generally bisexual, and often showy, are sometimes borne singly, as in some species of rose, or of the cloudberry (*Rubus chamaemorus*), or few or more together in a corymbose manner, as in some roses, hawthorne and others. The inflorescence in agrimony is a raceme, in *Poterium* a dense-flowered spike, in *Spiraea*, a number of cymes arranged in a corymb. The parts of the flowers are arranged on a pentamerous plan, with generally considerable increase in the number of stamens and carpels. The shape of the thalamus or floral receptacle, and the relative position and number of the stamens and carpels and the character of the fruit, vary widely and form distinguishing features of the different suborders, six of which may be recognized.

**Suborder I. Spiraeoideae** is characterized by a flat or slightly concave receptacle on which the carpels, frequently two to five in number, form a central whorl; each ovary contains several ovules, and the fruit is a follicle except in *Holodiscus*. The plants are generally shrubs with simple or compound leaves and racemes or panicles of numerous small white, rose or purple flowers. This suborder is nearly allied to the family Saxifragaceae, chiefly north temperate in distribution. The largest is *Spiraea*, numerous species of which are cultivated in gardens; *S. salicifolia* occurs in Britain apparently wild in plantations, but is not indigenous. The native British meadow-sweet is *S. Ulmaria*; dropwort is *S. Filipendula*.

**Suborder II. Pomoideae** is characterized by a deep cup-shaped receptacle with the inner wall of which the two to five carpels are united; the carpels are also united with each other, and each contains generally two ovules. The fruit is made up of the large fleshy receptacle surrounding the ripe ovaries, the endocarp of which is leathery or stony and contains one seed. The plants are shrubs or trees with simple or pinnately compound leaves and white or rose-coloured often showy flowers. The genera are distributed through the north temperate zone, extending southwards in the New World to the Andes of Peru and Chile. The largest genus, *Pyrus*, with about 65 species, includes apple (*P. Malus*), pear (*P. communis*), wild service (*P. torminalis*), rowan or mountain-ash (*P. aucuparia*) and white beam (*P. Aria*). *Mespilus* (medlar) and *Cotoneaster* are also included. (See separate articles for most of the above.)

**Suborder III. Rosoideae** is characterized by the receptacle being convex and swollen, as in strawberry, or cup-shaped, as in rose, and bearing numerous carpels, each of which contains one or two ovules, while the fruit is one-seeded and indehiscent. The genera are grouped in tribes according to the form of the receptacle and of the fruit. The Potentilleae bear the carpels on a large, rounded or convex outgrowth of the receptacle. In the large genus *Rubus* the ripe ovaries form drupelets upon the dry receptacles; the genus is almost cosmopolitan, but the majority of species occur in the forest region of the north temperate zone and in the mountains of tropical America. *R. fruticosus* is blackberry, *R. Idaeus*, raspberry, and *R. Chamaemorus*, cloudberry. In the flower of *Potentilla*, *Fragaria* (strawberry) and a few allied genera an *epicalyx* is formed by stipular structures arising at the base of the sepals. The fruits consist of numerous dry achenes borne in *Fragaria* on the much-enlarged succulent torus, which in the other genera is dry. In *Geum* (avens) and *Dryas* (an arctic and alpine genus) the style is persistent in the fruit, forming a feathery appendage

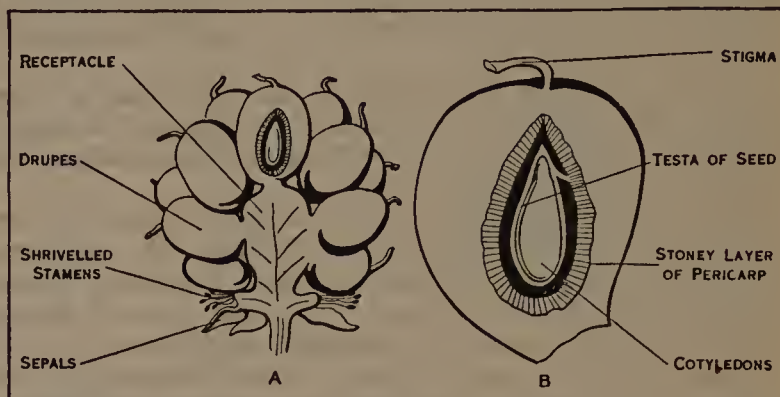


FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

DOG ROSE (*ROSA CANINA*), SHOWING VERTICAL SECTION OF COMPOUND FRUIT

(*Dryas*) or a barbed awn (avens), either of which is of service in distributing the fruit. The Potentilleae are chiefly north temperate, arctic and alpine plants.

The Roseae comprise the large genus *Rosa* (150 species), characterized by a more or less urn-shaped torus enclosing the numerous carpels which form dry one-seeded fruits enveloped in the bright-coloured fleshy torus. The plants are shrubs bearing prickles on the stems and leaves; many species have a scrambling habit resembling the brambles. The species of *Rosa*, like those of



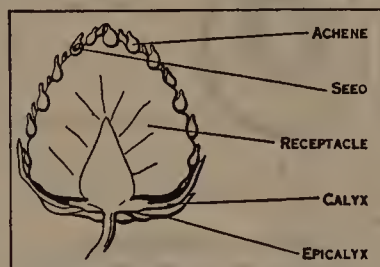
FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

BLACKBERRY (*RUBUS FRUTICOSUS*); SHOWING (A) VERTICAL SECTION OF COMPOUND FRUIT, (B) VERTICAL SECTION OF SINGLE DRUPE (ENLARGED)

*Rubus*, are extremely variable, and a great number of subspecies, varieties and forms have been described. Petals are often wanting, as in *Alchemilla* (lady's mantle) and *Poterium*, and the flowers are often unisexual and frequently wind-pollinated, as in salad burnet (*Poterium Sanguisorba*), where the small flowers are crowded in heads, the upper pistillate, with protruding feathery stigmas, and the lower staminate (or bisexual), with exserted stamens. *Agrimonia* (agrimony) has a long spike of small honeyless flowers with yellow petals; in the fruit the torus becomes hard and crowned by hooked bristles which ensure the distribution of the enclosed achenes.

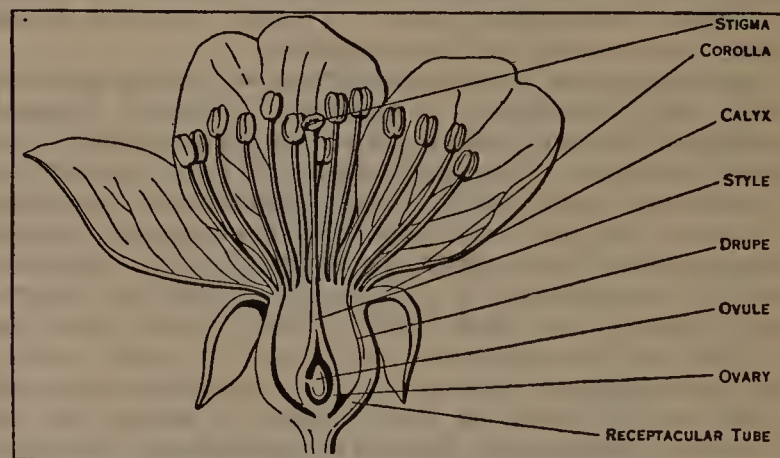
**Suborder IV. Neuradoideae** contains only two genera of desert-inhabiting herbs with yellow flowers; and the five to ten carpels are united together and with the base of the cup-shaped torus, which enlarges to form a dry covering round the one-seeded fruits.

**Suborder V. Prunoideae** is characterized by a free solitary carpel with a terminal style and two pendulous ovules, and the fruit a



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

STRAWBERRY (*FRAGARIA VESCA*), SHOWING VERTICAL SECTION OF COMPOUND FRUIT



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

VERTICAL SECTION OF FLOWER OF CHERRY

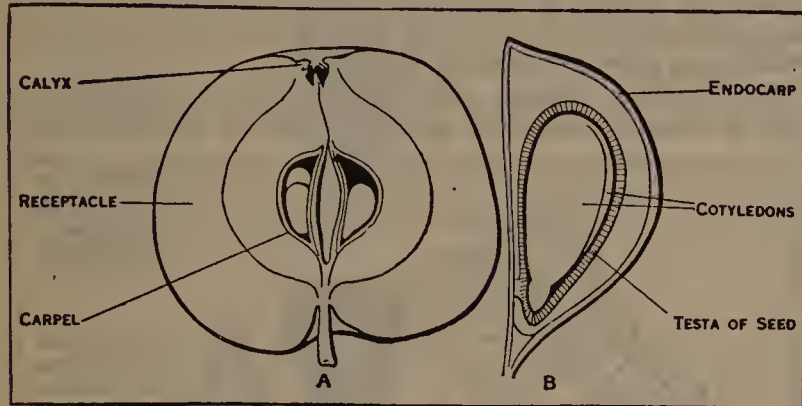
one-seeded drupe. The torus forms a cup from the edge of which spring the others parts of the flower. The plants are deciduous or evergreen trees or shrubs with simple leaves often with small caducous stipules, and racemes or umbels of generally showy, white or pink flowers. There are five genera, the chief of which is *Prunus*, to which belong the plum (*Prunus communis*), with several well-marked subspecies—*P. spinosa* (sloe or blackthorn), *P. insititia* (bullace), *P. domestica* (wild plum), the almond (*P. Amygdalus*) with the nearly allied peach (*P. persica*), cherry (*P. Cerasus*), birdcherry (*P. Padus*) and cherry laurel (*P. Laurocer-*



*asus*). The tribe is distributed through the north temperate zone, passing into the tropics.

**Suborder VI. *Chrysobalanoideae*** resembles the last in having a single free carpel and the fruit a drupe, but differs in having the style basal, not terminal, and the ovules ascending, not pendulous; the flowers are also frequently zygomorphic. The genera are tropical evergreen trees or shrubs, the great majority being South American.

In North America the family is represented by about 40 genera, the largest being *Crataegus* (hawthorn) with about 70



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS)

APPLE (*PYRUS MALUS*); SHOWING (A) VERTICAL SECTION THROUGH FRUIT, (B) ONE OF THE PARCHMENT-LIKE CHAMBERS, REMOVED FROM THE FRUIT CONTAINING A SEED

species, *Rubus* (bramble) with 40 species, *Potentilla* (cinquefoil, five-finger) with about 40 species, *Prunus* (plum, cherry, etc.) with 20 species, and *Rosa* with 15 species. *Potentilla* is the most generally distributed genus in the United States.

**DICOTYLEDONS**, in botany, the larger of the two great classes of angiosperms (*q.v.*), embracing most of the common flower-bearing plants. The name expresses the most universal character of the class, the importance of which was first noticed by John Ray namely, the presence of a pair of seed-leaves or cotyledons, in the plantlet or embryo contained in the seed. The embryo is generally surrounded by a larger or smaller amount of foodstuff (endosperm) which serves to nourish it in its development to form a seedling when the seed germinates; frequently, however, the whole of the nourishment for future use is stored in the cotyledons themselves, which then become thick and fleshy. In germination of the seed the root of the embryo (radicle) grows out to get a holdfast for the plant; this is generally followed by the growth of the short stem immediately above the root, the so-called "hypocotyl," which carries up the cotyledons above the ground, where they become the first green leaves of the plant. Protected between the cotyledons and terminating the axis of the plant is the first stem-bud (plumule of the embryo). The size and manner of growth of the adult plant show great variety, from the small herb lasting for one season only, to the forest tree living for centuries. The arrangement of the conducting tissue in the stem is characteristic; a transverse section of the very young stem shows a number of distinct conducting strands—vascular bundles—arranged in a ring round the pith; these soon become united to form a closed ring of phloem and wood, separated by a layer of cambium. In perennials the stem shows a regular increase in thickness each year by the addition of a new ring of wood outside the old one—for details of structure see **PLANTS: Anatomy**. A similar growth occurs in the root. This increase in the diameter of stem and root is correlated with the increase in leaf-area each season, due to the continued production of new leaf-bearing branches. A characteristic of the class is afforded by the complicated network formed by the leaf-veins,—well seen in a skeleton leaf, from which the soft parts have been removed by maceration. The parts of the flower are most frequently arranged in fives, or multiples of fives; for instance, a common arrangement is as follows,—five sepals, succeeded by five petals, ten stamens in two sets of five, and five or fewer carpels. An arrangement in fours is less frequent, while the arrangement in threes, so common in monocotyledons, is rare in dicotyledons. In some families the parts are numerous, chiefly in the case of the

stamens and the carpels, as in the buttercup and other members of the Ranunculaceae and in the Rosaceae. The characters of the flower and fruit are described in the articles **FLOWER**, **FRUIT** and **SEED**.

**BACILLARIALES or DIATOMS.** The diatoms are microscopic unicellular or colonial plants belonging to the Algae, and are especially distinguished by the complex structure of their cell-walls which are usually strongly impregnated with silica. The majority are exceedingly minute, and one with a length of  $\frac{1}{200}$  in. (0.125mm.) is well beyond the medium size. The first forms were discovered by O. F. Müller towards the close of the 18th century. With the perfection of modern microscopes and microscopic methods, the study of these minute plants has been prosecuted with great vigour and over 15,000 species of diatoms have been described, while about 1,200 species are known to occur in the fresh waters and on the coasts of Great Britain and Ireland.

**Structure.**—In spite of the immense number of diverse forms included in it, the class as a whole exhibits a remarkable uniformity of structure. The individual cells of diatoms are called *frustules*, and their wall consists of two similar halves (fig. 2), each composed of a slightly convex valve to whose incurved edges is attached at right angles a broad hoop-like connecting band. The two connecting bands together form the girdle. One half is slightly smaller than the other, the smaller fitting into the larger much as a box fits into its cover (fig. 2) and, according as one visualizes a circular, oval, or otherwise shaped box, one obtains a mental picture of the varied forms assumed by the frustules of diatoms; the sides of the box correspond to the connecting bands. As the protoplasmic contents increase in volume, the siliceous valves are pushed apart and the connecting bands become broader. Diatoms are usually described from two aspects, one in which the surface of the valve is exposed, the valve-view

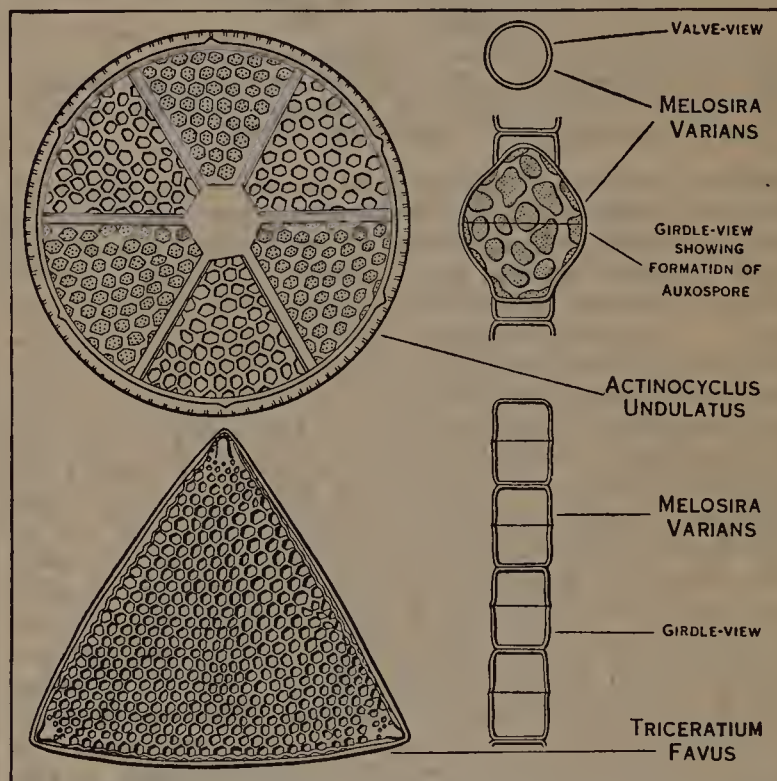


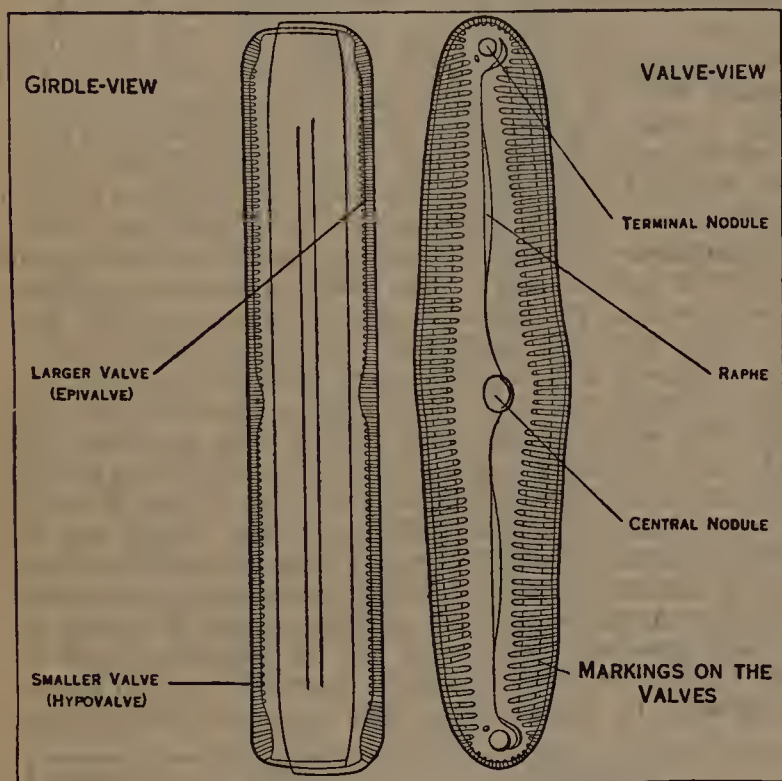
FIG. 1.—ALTHOUGH THERE ARE 15,000 KNOWN SPECIES, THE BACILLARIALES SHOW REMARKABLE UNIFORMITY OF STRUCTURE. THEY AVERAGE LESS THAN ONE TWO-HUNDREDTH OF AN INCH IN DIAMETER

(fig. 2); and one in which the girdle is exposed, the girdle-view (fig. 2). The valve-view exhibits great variety of form; the girdle-view is much more uniform and commonly rectangular. The valves may be circular (fig. 1), triangular (fig. 1), or oval in outline. Some are linear, as *Synedra ulna* (fig. 3); others (*Eunotia*), more or less crescentic; others again are wedge-shaped (*Podosphenia*, *Gomphonema*, fig. 3); some few have a sigmoid outline, as *Pleurosigma* (fig. 3); but the prevailing forms are boat-shaped (naviculoid), as in the genus *Navicula* (fig. 2), which embraces upwards of 1,000 species. A few genera have dorsiventral views (*Epithemia*, fig. 3).



Many diatoms are free-floating, but some (*Gomphonema*) are attached to foreign bodies by simple or branched gelatinous stalks. The frustules of some are connected to form ribbon-shaped colonies (*Fragilaria*) or zigzag chains (fig. 3 D). In a few genera numerous individuals are enclosed in a tube-like gelatinous envelope.

The valves are thin and transparent and generally ornamented with a variety of markings. The latter often appear as fine lines



FROM WEST, "ALGAE" BY PERMISSION OF THE CAMBRIDGE UNIVERSITY PRESS

FIG. 2.—EACH INDIVIDUAL CELL CONSISTS OF PARTS, THE SMALLER ONE FITTING INTO THE LARGER LIKE A BOX INTO ITS COVER. HERE IS SHOWN THE STRUCTURE OF A BOAT-SHAPED DIATOM

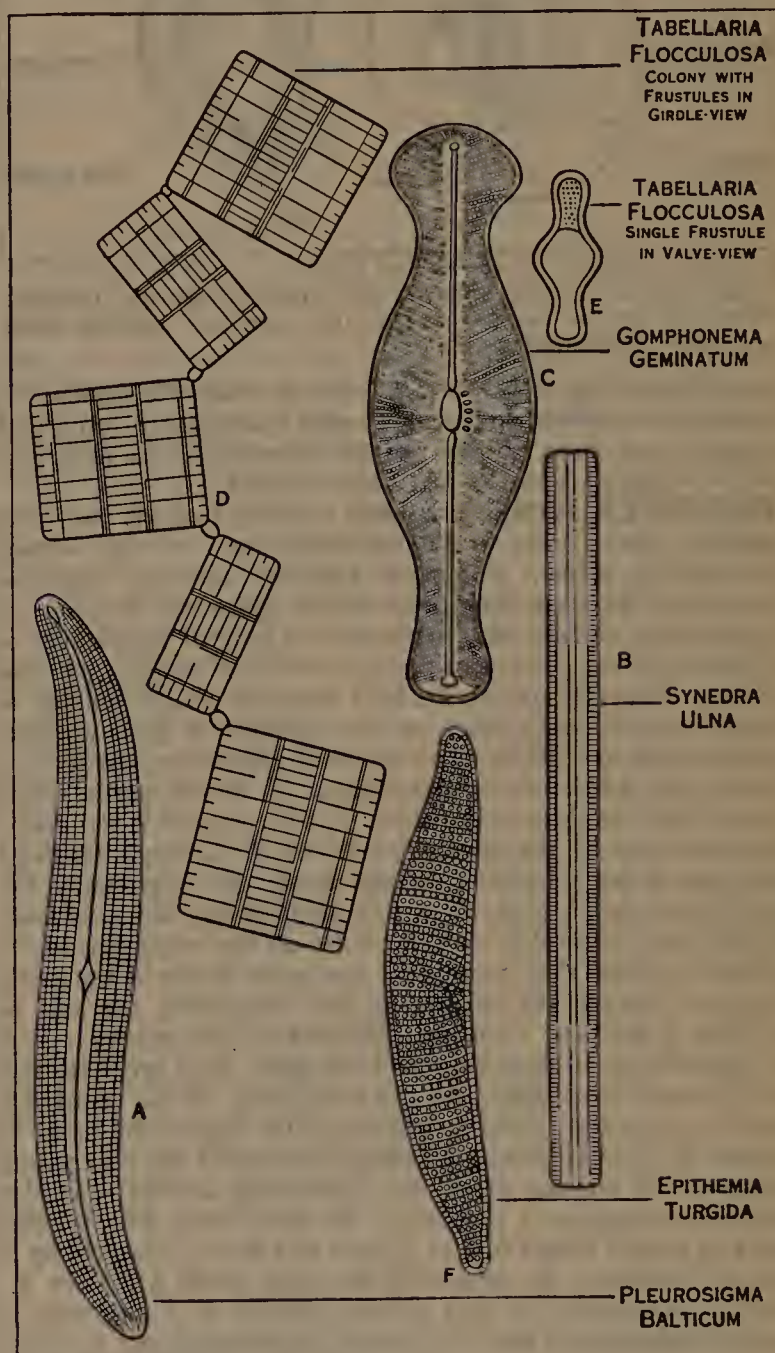
(striae) on the face of the valve, and the best lenses show them in many cases to consist of a series of separate dots (punctae) which correspond to small cavities within the siliceous wall. The valves of certain marine genera exhibit a beautiful areolated structure due to the presence of larger chambers within the wall (fig. 1). A good many diatoms, especially those of the navicula-type, have thickenings at the centre and at each extremity of the valve, known as nodules (fig. 2). These possess a complex structure and are generally connected by a long narrow cleft, the raphe (fig. 2), which appears as a straight or slightly undulating line in the valve-view. Some diatoms, while possessing nodules, lack a raphe, although in these cases the narrow area between the two rows of striae often simulates one (pseudoraphe).

The contents of diatom cells are very similar to those of other Algae. Beneath the wall there is a lining protoplasmic layer enclosing the cell-sap, and connected either by two broad bands or by a number of anastomosing strands with the central protoplasm in which the nucleus is embedded. The chromatophores are either one or two of large size, or numerous small lobed discs (fig. 1). The former often include a variable number of glistening pyrenoids. The characteristic brown colour is due to diatomin, a pigment resembling that of the brown Algae and masking the chlorophyll. The cells often contain abundant oil.

Many diatoms, but only those which possess a true raphe in their valves (*Navicula*, etc.), are able to move through the water, sometimes with considerable rapidity. The movements are doubtless in all cases related to the presence of the raphe, which in all probability contains streaming protoplasm connected with that in the interior of the cell by a complex system of canals within the nodules. Some believe that the movements depend upon an extrusion of mucilage from the region of the raphe. In *Cocconeis*, whose disc-shaped frustules are found attached in enormous numbers to *Cladophora* and other freshwater plants, only the valve in contact with the substratum possesses a raphe.

**Reproduction.**—The ordinary mode of multiplication is by cell-division, which usually occurs at night. The protoplasm divides into two masses and the halves of the cell commence to separate; thereupon fresh valves, which are at first very delicate, are secreted on the surfaces of the new protoplasmic masses opposite to the valves of the parent. The new valves are situated within the girdle of the original frustule, but as their own connecting bands develop, those of the parent separate. Each of the new individuals thus has one valve derived from the parent, and one that is newly formed and more or less parallel to it. This process of division is repeated at frequent intervals, and it has been calculated that from a single frustule 1,000,000,000 new individuals may arise in the course of a month.

The individual diatom, owing to the rigidity of the siliceous wall, is ordinarily incapable of any increase in length and, since



C AND D FROM SMITH, "BRITISH DIATOMACEAE"

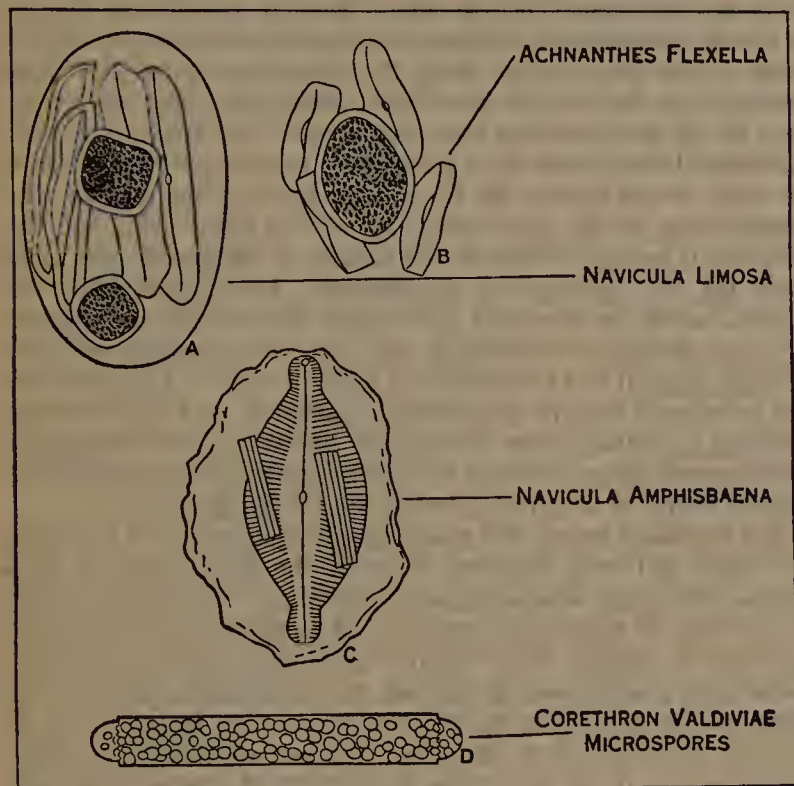
FIG. 3.—VIEWED FROM THE VALVE SIDE, BACILLARIALES EXHIBIT GREAT VARIETY OF FORMS. SOME HAVE A SIGMOID OUTLINE (A), SOME ARE (B) LINEAR, (C) WEDGE-SHAPED, OTHERS (D) FORM ZIG-ZAG CHAINS, WHILE OTHERS ARE CIRCULAR, OVAL, ANGULAR

the new valves are always formed within the girdle of the old ones, it would follow that one individual of every succeeding generation is reduced in length by the thickness of the girdle. This is not, however, strictly true, as daughter cells are sometimes formed which are larger than the parent cell, so that the reduction in size is not always proportional to the number of divisions.

It seems that often, when the diminution in size has reached a limit, the maximum size is regained by the formation of *auxo-*



*spores*, but other conditions than this no doubt also lead to auxospore production. Auxospores in many cases arise as a result of the fusion of two individuals; prior to this conjugation, the protoplasmic contents of each may divide into two parts. The two halves of each frustule then separate, and the liberated contents fuse to form one (fig. 4 B) or two (fig. 4 A) auxospores, which are surrounded by the empty valves of the original individuals. In other cases, however, auxospores are formed merely from the



FROM WEST, "ALGAE"

FIG. 4.—THE MODE OF MULTIPLICATION IS BY CELL DIVISION. THE PROTOPLASM DIVIDES INTO TWO MASSES AND THE HALVES SEPARATE. THE LIBERATED CONTENTS FUSE TO FORM ONE (B) OR TWO (A) AUXOSPORES. SOME (C) FORM WITHOUT FUSION WHILE OTHERS (D) FORM NUMEROUS MICROSPORES WHICH ARE LIBERATED AS NAKED CELLS

contents of a single individual without any process of fusion (fig. 4 C), and this is invariably their mode of formation in centric diatoms (fig. 1). The auxospores usually undergo enlargement and then, after secreting new valves, constitute a new individual.

In some marine centric diatoms the protoplasmic contents at times divide to form numerous *microspores* (fig. 4 D), which are liberated as naked cells, in some cases provided with cilia like the sexual cells (gametes) of Algae. It is not impossible that they represent the sexual cells of these, but the evidence is inconclusive.

**Affinities and Classification.**—The diatoms have been held to be allied to the brown Algae (Phaeophyceae) but, apart from the similarity in colour, there is little to support such a view. On the other hand there are some marked points of resemblance to Heterokontae (see ALGAE) which may indicate a remote relationship. The obvious resemblances to Conjugatae seem to be the result of a parallel development.

The system of classification of diatoms usually followed is one put forward by Schütt (1896). He separates them into two primary divisions, the Centricae and the Pennatae. The former include the diatoms in which the valve view possesses a radial symmetry around a central point, and which are destitute of a raphe (or pseudoraphe) (fig. 1). The Pennatae comprise those in which the valve-view is boat- or needle-shaped, with the markings arranged on either side of a median line (raphe or pseudoraphe) (fig. 3). The Centricae are much more abundant in the sea than in fresh waters. It is possible that these two groups are not as nearly related to one another as has hitherto been supposed. In particular the fact that the sexual reproductive process appears quite different in the two cases makes a close affinity doubtful.

**Mode of Preparation.**—Diatoms are usually gathered in small bottles, as free as possible from extraneous matter. The material is next boiled with acid (either hydrochloric, nitric, or sul-

phuric) in order to eliminate all foreign matter and dissolve away the non-siliceous parts of the frustules. The residuum is treated with an excess of water, well shaken and allowed to settle, after which the supernatant liquid is carefully removed with a syringe; it is necessary to repeat this treatment till all traces of the acid have been removed. Subsequently the sediment may be boiled with carbonate of soda, the alkali being removed in the same way as the acid. A small portion is then placed on a glass slide and, when the moisture has fully evaporated, the remaining film is covered with dilute Canada balsam, dammar, or styrax, and a thin cover-glass gently laid on top.

**Occurrence and Distribution.**—The conditions necessary for the growth of diatoms are moisture and light, and wherever these coexist, these forms will almost invariably be found. They occur abundantly in cultivated soils, and mixed with other forms on the surface of moist rocks; in pools and other small pieces of water they form a brownish stratum on the surface of the mud, or cover the stems and leaves of water plants or floating twigs with a furry investment. Marine forms are usually attached to seaweeds, and many are found in the stomachs of molluscs, holothurians, ascidians, and other denizens of the ocean. Both in fresh waters and in the sea, moreover, there are myriads of free-floating diatoms which at times indeed make up the main bulk of the plankton. Diatoms are most abundant in cold latitudes, having a general preference for cold water, and exist in prodigious numbers in the Arctic and Antarctic oceans. The freshwater species are almost always distinct from those found in salt or brackish water.

Large numbers of fossil diatoms are known. Since the siliceous wall is practically unperishable, it persists after the death of the individual, so that where diatoms occur abundantly there is an unceasing rain of their minute valves on to the bottom of sea or lake as the case may be. In this way extensive deposits of diatomaceous earth may arise, and such are not only being formed at the present time, but have been produced abundantly in the past. Even when such deposits have been hardened into solid rock, the frustules remain unaltered, and from their character it is often possible to arrive at conclusions as to the conditions under which the deposit was formed. These earths are generally of a white or grey colour, and mostly soft and friable. They are used as polishing powders (Tripoli), as absorbents for nitroglycerine in the manufacture of dynamite (Kieselguhr), in the preparation of dentifrices, and in the manufacture of non-conducting and sound-proof materials. Most of the fossil deposits are in Tertiary rocks, although there are records of diatoms in the Trias.

Vast deposits of diatomaceous earths have been discovered in various parts of the world, some of freshwater, others of marine origin. That at Richmond in Virginia (U.S.A.), extends for many miles and is in places at least 40ft. deep, whilst in the western states of America beds of 300ft. thickness have been discovered. Other, though less extensive, deposits are known at Dolgelly (Wales) and at Bilin in Bohemia. It is a remarkable fact that the fossil genera and species are very similar to and in part quite identical with the living representatives of the class.

**BIBLIOGRAPHY.**—For a general account of diatoms see G. S. West and F. E. Fritsch, *British Freshwater Algae* (1927); or the section dealing with those forms in F. Oltmanns, *Morphologie und Biologie der Algen* (Jena, 1922). There are numerous systematic works for the determination of diatoms, e.g., W. Smith, *A Synopsis of the British Diatomaceae* (1853–56); Adolf Schmidt, *Atlas der Diatomaceenkunde* (Leipzig, 1874 and onwards), a very extensive iconographical work; H. van Heurck, *Synopsis des Diatomées de Belgique* (Antwerp, 1880–85); H. von Schönfeldt, "Bacillariales" in A. Pascher, *Süsswasserflora Deutschlands, Österreichs, und der Schweiz* (Jena, 1913) and F. Meister, "Kieselalgen der Schweiz" in *Kryptogamenflora der Schweiz* (Part iv. 1912). (F. E. F.)

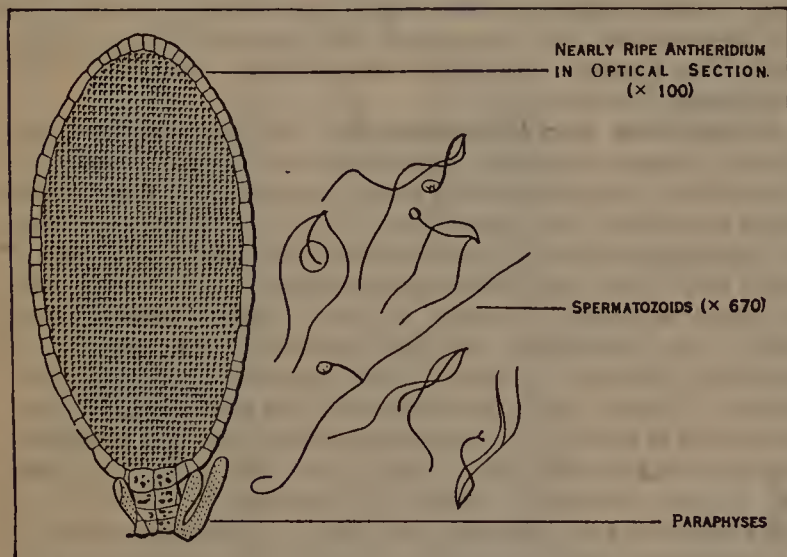
**PANICLE**, in botany the name given to an inflorescence which is a compound raceme (*q.v.*) as in oats. (See also FLOWER.)

**PERIANTH**, the term used in botany to denote the outer covering of the flower, composed of more or less modified but non-reproductive leaves and divided usually into an outer, often greenish whorl, the calyx of sepals; and an inner, often brightly-coloured whorl, the corolla of petals. (See FLOWER.)

**BRYOPHYTA**, the botanical name of the second great subdivision of the vegetable kingdom. The plants in this group are



all small, some, indeed, so minute that only the most careful observer is aware of the great variety of form and structure shown by them. It is quite common for liverworts, mosses, and even small plants of much higher groups to be indiscriminately classed together and popularly called "mosses." The Bryophyta do, however, form a well-defined class, easily recognizable with a little care, and it is equally easy to distinguish the broad sub-



FROM STRASBURGER, "TEXT-BOOK OF BOTANY," BY PERMISSION OF MACMILLAN & CO.

FIG. 1.—MARCHANTIA POLYMORPHA, SHOWING THE ANTHERIDIUM, WHICH GIVES RISE TO THE MALE ELEMENT IN THE PROCESS OF REPRODUCTION OF CERTAIN MOSS AND LIVERWORT PLANTS

groups into which they naturally fall. Their study necessarily entails minute observation, yet such observation shows them to be of great scientific interest, presenting as they do a special type of life history and affording in some of their groups graphic evidence of their evolutionary trend in spite of the complete absence of reliable evidence from fossil remains of any antiquity.

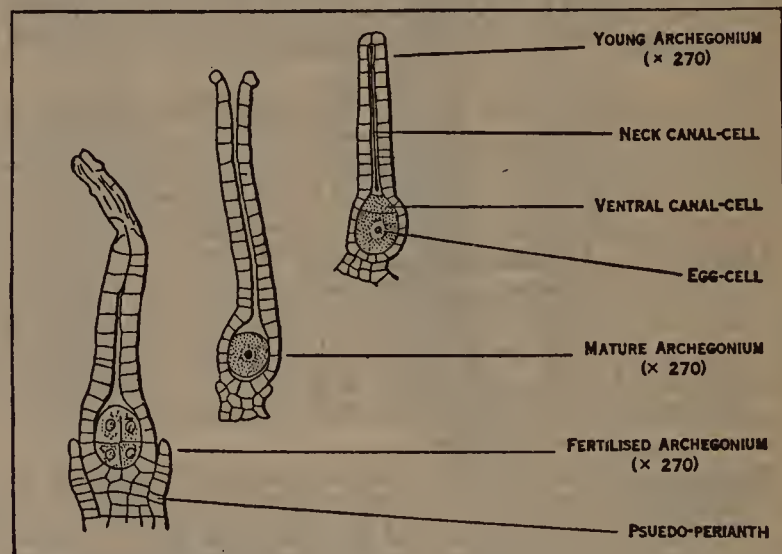
Speaking generally, Bryophyta grow only under moist conditions, being commonly found along the sides of ditches, banks of streams and similar places. Some can certainly grow in even what would appear to be quite dry situations, though it would be more correct to say that such forms can exist through more or less prolonged dry periods, but grow actively only when conditions are comparatively moist. Even fewer are those forms which can thrive only in or on water. Liverworts and mosses are widely distributed throughout the world and with careful search it is possible to find representatives of a wide range of forms in almost any district. Usually they occupy a subordinate place in the general vegetation but occasionally, as with bog-mosses and some arctic mosses, they dominate the vegetation.

**General Structure.**—Mosses and most liverworts, amidst all their variety of form, are similar in so far as the plant as we see it consists of a stem bearing leaves (see figs. 7, 11). Some liverworts show no differentiation into stem and leaf, but appear as flat structures closely pressed to the substratum on which they grow (figs. 3, 4). Such a habit we describe as thalloid; the plant is a thallus (i.e., a structure showing no differentiation into leaf and stem) in contradistinction to the leafy shoot of the remaining liverworts and mosses; though few in number of forms, those with this thalloid habit are very widely spread and are exceedingly interesting and significant in their form and structure. The small leafy shoot or thallus, as we see it, is self-supporting, possessing chlorophyll as do other plants and rhizoids—elongated cells resembling root hairs which grow from the underside of the plant and not only attach it to the soil but convey necessary salt solutions therefrom. Most interesting of all is the fact that the liverwort and moss plant bear the reproductive organs called antheridia and archegonia. The *antheridium* when mature has a shorter or longer stalk supporting a spherical or more usually an ovoid body which consists of a wall of flattened cells enclosing a densely packed mass of very small cubical cells (fig. 1). In all cases examined, each of these cubical cells gives rise by division to two motile bodies called spermatozoids and functioning as the male element in sexual reproduction. Each

spermatozoid consists of a more or less spirally coiled, club-shaped body, pointed at its anterior end and bearing there two long cilia whose movements are responsible for the motility of the sperm. These spermatozoids are liberated from the antheridium by degeneration of the walls enclosing them. The *archegonium* also usually has a stalk and takes the form of a minute, long-necked flask (fig. 2). The wall of the flask consists of a layer of cells enclosing the ovum or egg-cell, the ventral canal cell and a row of neck canal cells. The ovum or egg-cell, the female element in sexual reproduction, occupies the lower part and most of the space of the body of the flask, the remaining upper part being occupied by the ventral canal cell, whilst the space within the neck of the flask is filled by a row of cells, the neck-canal cells, the whole being closed by a lid of cells continuous with those of the wall. When mature the lid is burst open by the mucilaginous degeneration of the neck-canal and ventral-canal cells, and fertilization is brought about by the passage of the motile spermatozoids via the mucilage to the egg-cell. In all probability the spermatozoids are attracted to the open neck of the archegonium by some chemical stimulus; in any case one spermatozoid fuses with the egg cell and fertilization is brought about. The antheridia and archegonia arise by division of a single cell, and though almost identical in mature form throughout liverworts and mosses, the development differs in detail in the two groups. These differences may be found in literature cited in the bibliography.

The fertilized ovum, two nuclei fused together, is the beginning of a new and very different stage in the life-history of these plants. This stage when completely developed varies considerably in structure in the various groups, but in general terms we may say that it consists of a capsule containing spores, sometimes borne upon a stalk, and throughout its whole life borne upon and nourished by the plant on which it arose (see figs. 4, 11). In spite of the variation in structure, the end of this stage of the life-history is in all cases the production of spores which are shed and germinate in course of time. In mosses the spore gives rise to a branched filament of cells, the *protonema*, upon which the new moss plant arises. In liverworts a protonema is scarcely recognizable, the spore growing directly into the new plant.

**Life-History.**—Here then, as in all plants higher in the scale of botanical classification, the life-history is divisible into two stages which follow each other with regular alternation. The



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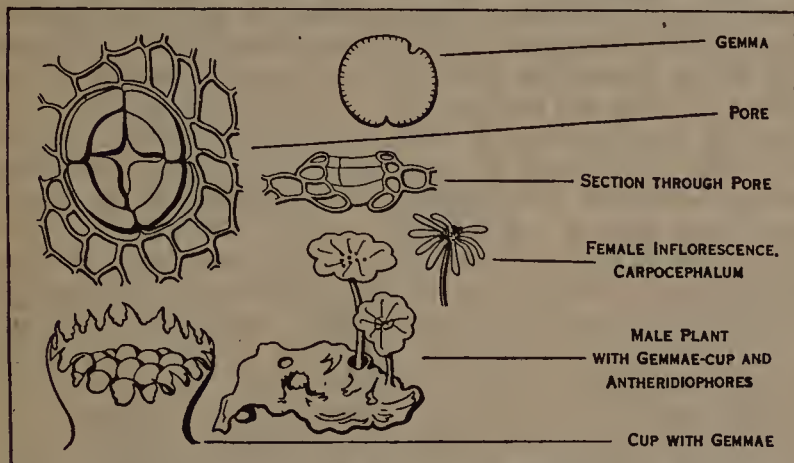
FIG. 2.—MARCHANTIA POLYMORPHA, SHOWING THE ARCHEGONIUM, WHICH ENCLOSES THE OVUM OR EGG CELL

plant as we see it in the field begins its life with the spore, eventually produces antheridia and archegonia and ends that stage when a spermatozoid fuses with an ovum. This stage we call the *gametophyte*. The second stage begins with the fertilized ovum, develops into a capsule sometimes stalked, and attached to the gametophyte by a foot—the whole structure being called a *sporangium*—and ends with the production of spores. This stage we know as the spore-bearing stage or *sporophyte*. The life-history of a liverwort and moss then consists of the regular alternation of gametophyte and sporophyte. In this life-history the



interest lies in the fact that the plant as we see it is the gametophyte, the sporophyte dependent upon it and commonly recognized as the moss "fruit" being the subordinate phase in this sense. In all other plants higher in the scale of evolution, the reverse is the case, the independent self-supporting plant is the sporophyte, the gametophyte being the subordinate partner in the life cycle, and though not always dependent upon the sporophyte, always comparatively inconspicuous (see PTERIDOPHYTA and CYTOLOGY for discussion of the fundamental nuclear difference between haploid gametophyte and diploid sporophyte).

The Bryophyta, according to their form and structure, can be subdivided into the Hepaticae (liverworts) and Musci (mosses).



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FIG. 3.—*MARCHANTIA POLYMORPHA*. A LIVERWORT WELL ADVANCED IN THE GROUP THAT SHOWS NO DIFFERENTIATION IN STEM AND LEAF

Further, the Hepaticae are clearly divisible into three smaller groups, the Marchantiales, Jungermanniales, and Anthocerotales, whilst the Musci also fall into three well-marked groups, the Sphagnales, Andreaeales, and Bryales.

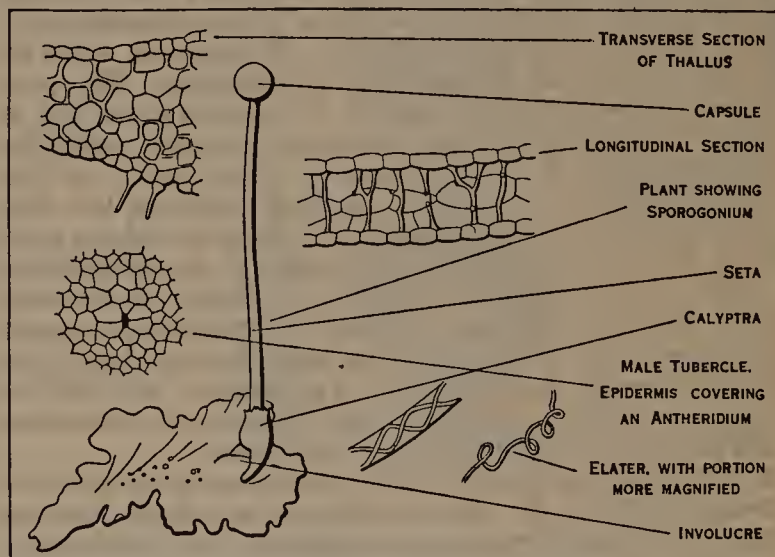
#### HEPATICAEE

The three groups into which liverworts are botanically divided show among their several members lines of progression in three different directions from a basal, simple type more or less common to them all. Stated broadly, evolution in liverworts has progressed from a common form along three distinct lines. From such a simple type, for instance, the Marchantiales have moved along the line of increasing complexity in texture of the thallus, the Jungermanniales have retained the simplicity of texture but show an increasing tendency to discard the thalloid and assume a leafy-shoot habit, whilst the Anthocerotales have retained both the simple texture and habit of the thallus but developed a peculiar sporogonium. These tendencies require fuller discussion.

**Marchantiales: Structure.**—Of the Marchantiales, the genus *Riccia*, with a world-wide distribution and including many species, affords the simplest organization of the group. *Riccia* consists of a flat, dichotomously-branched thallus growing appressed to the ground, attached thereto by rhizoids. The growing apex lies at the base of a heart-shaped cleft at the end of the thallus, the two lateral lobes being produced by the enlargement of cells cut off from the apical cell or cells. This thallus is thickest in its middle line but thins out towards the edges; its upper half consists of vertical columns of green chlorophyll-containing cells, its lower half of cells comparatively free from chlorophyll irregularly crowded together and acting as storage cells for the food manufactured by the upper assimilating half. Provision for aeration has here its lowest expression, being represented merely by small spaces between the vertical rows of cells in the upper half of the thallus. On the lower surface one finds the hair-like structures, rhizoids, already mentioned, and of these two types may be recognized, smooth and tuberculate. The latter, as their name implies, possess many small pegs of cellulose projecting into the cavity from the wall of the cell. In addition to rhizoids on the underside there are present small scales or plates of cells which we call ventral scales or amphigastria. *Riccia* is peculiar in that the ventral scales arise singly from the growing point and are later torn into more by lateral expansion of the thallus, whereas in all other Marchantiales forms, they arise in pairs—a fact of

possibly great theoretical significance. *Corsinia* gives us a step in advance in texture of the thallus. Here the upper part of the thallus shows well-developed air chambers bounded on all sides by plates of cells, below by the storage tissue and roofed in by an epidermal layer of cells; each chamber is open to the air by a simple pore. *Reboulia* shows much the same structure, but in *Fegatella* we meet a further advance in complexity. The air chambers here are very evident as in *Corsinia*, they open by a simple pore in just the same way but the space within the chamber is crowded with small columns of cells projecting into the cavity from its floor. These columns of cells are bathed by air and are packed with chlorophyll-bearing plastids. A still further advance is shown by *Preissia* and *Marchantia*. Here the thallus, air chambers and assimilating filaments are the same as in *Fegatella*, but the pores are very different. The pore in the epidermal roof of the air chamber takes the form of a small barrel with both ends open; the cells forming the sides, on occasions of drought, close the lower end of the barrel, which projects into the cavity (fig. 3).

**Marchantiales: Gametophyte.**—Alongside this progression in thallus complexity go other striking features. In *Riccia* the antheridia and archegonia are scattered irregularly over the upper surface of the thallus, sunk in the vertical columns of assimilating tissue, or if there is any sign of grouping of these reproductive organs it is very indefinite. *Corsinia* has separate male and female plants, and the male are very scarce and difficult to find even in a fruiting culture. The archegonia occur in groups and they come to lie in a saucer-shaped depression in the upper surface of the thallus. Furthermore, after an egg-cell is fertilized a small region of thallus tissue behind the archegonium grows rapidly and results in an irregular hood overhanging the sporogonium. This hood foreshadows a dominant feature of higher forms. In *Plagiochasma* we see a further advance. Both antheridia and archegonia are usually found in the same plant, the antheridia commonly formed first and appearing grouped together on small button-shaped masses of tissue along the dorsal surface of the thallus. The archegonia are also produced in compact groups, but here the portion of thallus bearing them grows up quickly and results in a stalked structure externally much like a miniature mushroom. This stalked mass of thallus tissue lifts up the archegonia which become displaced to the under edge of the cap and forms the



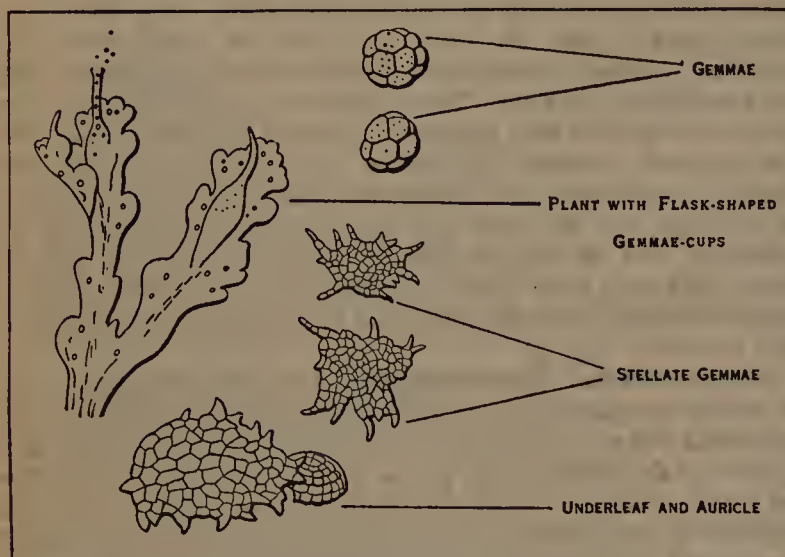
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FIG. 4.—GENERAL STRUCTURE OF THE *PELLIA EPIPHYLLA*, THE COMMONEST GENUS OF THE SIMPLE ANACROGYNÆ

structure we call an *archegoniophore* or more usually a *carpocephalum*. Here in *Plagiochasma* it arises on the dorsal surface behind the apex and is simply a dorsal outgrowth. In *Grimaldia* we have still further advance. A dorsal carpocephalum is formed as in *Plagiochasma*, but its formation stops the growth of the thallus apex and further growth is by a ventral branch. From this stage it is but a step to *Reboulia* where a carpocephalum is formed very much like *Plagiochasma*, but we find that there is a groove running up the stalk and branching in the cap, and that these grooves are packed with rhizoids. In short the apical cell



of the thallus has been utilized in the formation of the carpocephalum which is now a branch of the thallus and no longer a dorsal outgrowth. *Preissia* and *Marchantia*, especially the latter, reach the extreme development in this respect. Here the antheridia are borne on stalked apical structures, *antheridiophores*, the antheridia being embedded in the upper surface of the cap. Both antheridiophores and carpocephala have grooves packed with



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FIG. 5.—*BLASIA PUSILLA*, A LIVERWORT WHICH PRODUCES TWO TYPES OF GEMMAE, ONE OF WHICH GROWS INTO A NEW PLANT

rhizoids; they are branch structures and further growth of the thallus must be by ventral branch (fig. 3).

**Marchantiales: Sporophyte.**—The sporophyte generation increases in complexity along the same line. In *Riccia* the sporophyte is again in its simplest form, consisting of a spherical body which is just a single wall of sterile cells enclosing nothing but spores. This simple sporogonium is sunk in the tissue of the thallus and is surrounded by a double layer of cells, the calyptra, derived from the venter of the archegonium. Spore discharge is afforded by decay of gametophyte tissue and wall of sporogonium. In *Corsinia* the sporogonium is not sunk in the thallus tissue, and has, in addition to the *Riccia*-like structure of its sporogonium, sterile cells intermixed with the spores and a definite mass of sterile cells, the foot, attaching the sporogonium to the thallus. In higher forms the tendency to differentiation within the sporophyte generation reaches its fullest expression. The sporogonia are borne beneath the cap of the carpocephalum and all possess a foot, and in addition to spores have peculiar sterile cells. These nourish the developing spores and when mature are elongated and have one or two spiral bands of thickening laid down inside their walls. They are sensitive to moisture and are called *elaters*. We also find additional protection of the sporogonium. In most of them flap-like outgrowths of tissue, the *involute*, sheathe the young sporogonia whilst in *Marchantia* each sporogonium possesses a sleeve of tissue growing from the base of the archegonium—the *pseudoperianth*. Furthermore, we find that attempts are made at the formation of caps to the sporogonia which are cast off at the time of spore discharge.

It is thus possible to trace a serial progression in the genera of liverworts placed in the Marchantiales, the progression involving thallus, reproductive organs and sporogonia. The Marchantiales also afford us examples of vegetative or asexual reproduction. In the lower forms we seldom find definite structures set apart as asexual reproductive bodies though they are present here and there—generally any branch of the thallus may become detached by decay of older parts and thus lead to increase in number of plants. *Marchantia*, however, has definite buds, or *gemmae*, which are multicellular bodies, in shape much like the base of a fiddle, borne in large numbers in circular cups on the upper face of the thallus (fig. 3). Each gemma can reproduce a new plant. *Lunularia* has similar gemmae-cups, though these are semilunar in shape.

The *Jungermanniales* do not show such a neat progression in structure as the Marchantiales. They show progression from the

simple thalloid type towards the leafy habit and fall easily into two groups, the Anacrogynae and the Acrogynae.

**Anacrogynae.**—The Anacrogynae afford us the simplest types of the whole group. There is an absolute lack of tissue differentiation in all forms, but an obvious effort to differentiate in the thallus a rhizomatous portion and a specialized assimilating portion. The genus *Pellia* is at once perhaps the most common and certainly the simplest, if one omits *Sphaerocarpus* and *Riella* which cannot be here described. In *Pellia* (fig. 4) the thallus is just like that of the Marchantiales in outline but has no air pores, or chambers, and so appears perfectly smooth and green. No definite ventral scales are formed and no tuberculate rhizoids. These peculiar rhizoids are possessed only by the *Marchantiales*. The antheridia are spherical bodies borne scattered over the upper part of the thallus; the same thallus bears archegonia in groups behind the apex and protected by an involucre in the form of a shield of tissue growing up from behind and stretching forward as a little pocket over the archegonia. The sporogonium when mature consists of a basin-shaped foot embedded in the thallus and a long stalk or seta bearing a capsule. Within the wall of the capsule we find spores intermixed with elaters which in *Pellia* radiate from a column of sterile cells projecting into the capsule from the base, the *elaterophore*. As a well-developed sheath around the base of the seta may be seen the calyptra, the remains of the archegonium which developed after fertilization and through which the sporogonium burst as the seta elongated. At maturity the spores are discharged by a splitting of the wall of the capsule along four lines from the apex, resulting in four valves which curl back and expose the spores and elaters. With the exception of the elaterophore, the sporogonium of *Pellia* may be taken as typical of all the Jungermanniales, Anacrogynae and Acrogynae, for its structure is at once exceedingly uniform throughout the group and in sharp contrast with that of the Marchantiales. In the latter the stalked carpocephalum is gametophytic tissue whereas in the Jungermanniales the stalk which serves exactly the same purpose is sporophytic tissue.

From *Pellia* as a basal type we can trace in the Anacrogynae an attempt at the assumption of a leafy habit but it never reaches any high degree of organization. The apparent leafiness is rather a result of a more or less pronounced lobing of the thallus or a branching of the thallus. *Petalophyllum* and *Fossombronia* (fig. 6) give us the best attempt in this direction. Apart from this feature, the Anacrogynae are very uniform in structure; they differ in detail rather than in basic characters. Many forms possess methods of asexual reproduction highly developed. *Blasia*



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FIG. 6.—*FOSSOMBRONIA PUSILLA* IN WHICH THERE IS AN UNSUCCESSFUL ATTEMPT AT ASSUMING A LEAFY HABIT

*pusilla* (fig. 5), a monospecific genus which very seldom forms sexual organs, is very striking in this respect. This plant produces two types of gemmae, one in the form of little scales which become detached and grow into a new plant, the other takes the form of multicellular gemmae produced in large numbers in beautiful "Florence flasks," formed near the apex of branches of the thallus. *Aneura* and some species of *Metzgeria* have a peculiar method of non-sexual reproduction, the cells of the thallus producing two non-motile gemmae in each cell, their liberation being by breakdown of the cell within which they arose.

The one fundamental fact in their organization which sharply distinguishes the Anacrogynae from the Acrogynae is that the apical cell is never involved in the formation of the archegonia; in other words the archegonia and sporogonia are never apical on main or lateral shoots, but always dorsal.

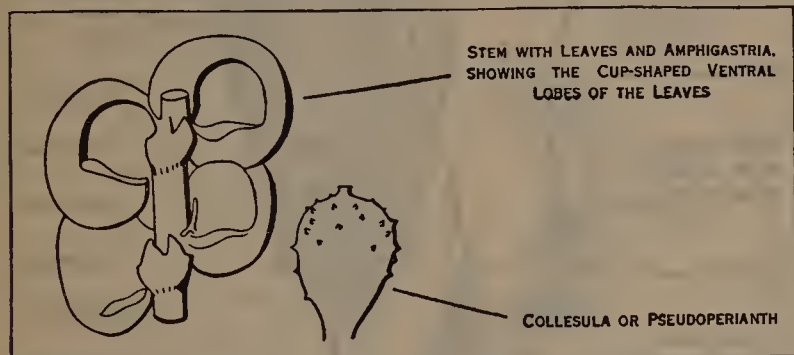
**Acrogynae.**—In the Acrogynae, though the antheridia are never apical, the archegonia always are so, on either main or lateral shoots. The apical cell is used in the formation of archegonia and further growth of the shoot is by a ventral branch. Again the Acrogynae, although including in their number quite 95%



of all known species of liverworts, are very uniform in plan, though differing in detail. They are all leafy types, commonly known as leafy or foliose liverworts. Their leaves are always definitely related to the divisions of the usual three-sided apical cell of the shoot and in their highest development occur in three rows. Of these three rows of leaves two different sets are recognizable. The Acrogynae are still dorsiventral in habit and two of the three rows of leaves occur in a dorsilateral position, exposed to the light, whilst the third row occurs on the ventral side of the shoot and its members are always smaller in size and usually different in shape from the other leaves. These distinct ventral leaves are called *amphigastria* (fig. 7). In some cases amphigastria are absent as in *Diplophyllum*, *Scapania* and some *Lejeunias*. The upper leaves are commonly more or less lobed, a two-pronged leaf being very common and their insertion on the stem is a point of importance. They may be inserted transversely with reference to the axis of the shoot; they may be obliquely inserted so that the edge of one leaf overlaps the edge of the next—if they overlap like the tiles of a roof they are said to be incubus, if the reverse they are succubus.

With regard to sexual organs, some Acrogynae are dioecious, some monoecious, sometimes they occur on special branches, sometimes not. The antheridia are never apical, they always occur in numbers along the stem, most commonly in the axils of leaves of the main shoots, in which case the leaves usually become hollow or hooded and protect them. The archegonia are sometimes on main shoots, sometimes on special shoots; in either case they always terminate the stem. The leaves near the archegonia are always modified and this modification extends often to three or four pairs of leaves—usually they become larger and simpler than the stem leaves and form the involucre. We often find in forms where amphigastria are normally absent that one is produced near the involucre. Very few cases are known where amphigastria are entirely absent (*Scapania*). Where they do occur on the stem, in the involucre they are often as large as the stem leaves themselves though usually simpler in form. Within the involucre we commonly find a tubular body, the *collesula* or *pseudoperianth* (fig. 7), which, though tubular in its origin and development, is referred to a coalescence of three leaves, the two dorso-lateral and the amphigastrium. Few families lack a collesula.

The sporogonia in the foliose liverworts are, apart from detail, much like those in the Anacrogynae, consisting of a foot, long seta



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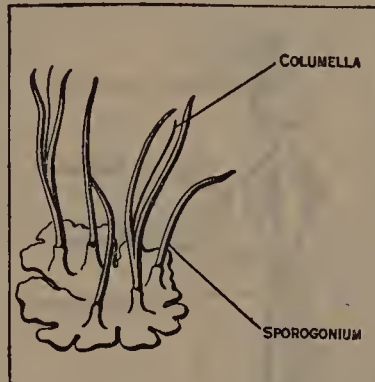
FIG. 7.—*FRULLANIA DILATATA*, A GENUS OF THE ACROGYNÆ, A GROUP WHICH INCLUDES 95% OF ALL KNOWN SPECIES OF LIVERWORT AND WHOSE MEMBERS ARE COMMONLY KNOWN AS LEAFY LIVERWORTS

and capsule opening by four slits from the apex and containing spores and elaters. A tendency widely spread has been the expansion of the foot as mentioned in *Pellia*. This prevalent expansion of the foot is connected with another feature shown by some of the foliose liverworts. The tissue around the foot becomes involved in the expansion and this ultimately resolves itself into the formation of a conspicuous pouch or *marsupium* which hangs down from the tip of the stem, has many rhizoids on its outer basal portion and within bears the archegonia and subsequently the foot of the sporogonium at the base of the pouch.

Many of the Acrogynae possess wonderful modifications in relation to water storage. *Trichocolea*, a genus found in sheets at the base of trees in wet tropical jungles, has leaves which are much branched and filamentous, reminding one of the dissected leaves

of ordinary water plants. Pouch formation by the leaves is very common. In *Frullania* (fig. 7) the ventral lobe of the leaf forms a beautiful pouch; in others, as in some *Lejeunias* and *Radulas* the two lobes of the leaf approach to form a cup. *Physotium giganteum* has peculiar leaves the ventral lobe of which is just like a bottle, the dorsal lobe being hollowed out and leading directly into the orifice of the bottle. *Physotium acinosum* has replaced leaf bottles by collesula bottles, which only rarely contain archegonia but are solely for water storage.

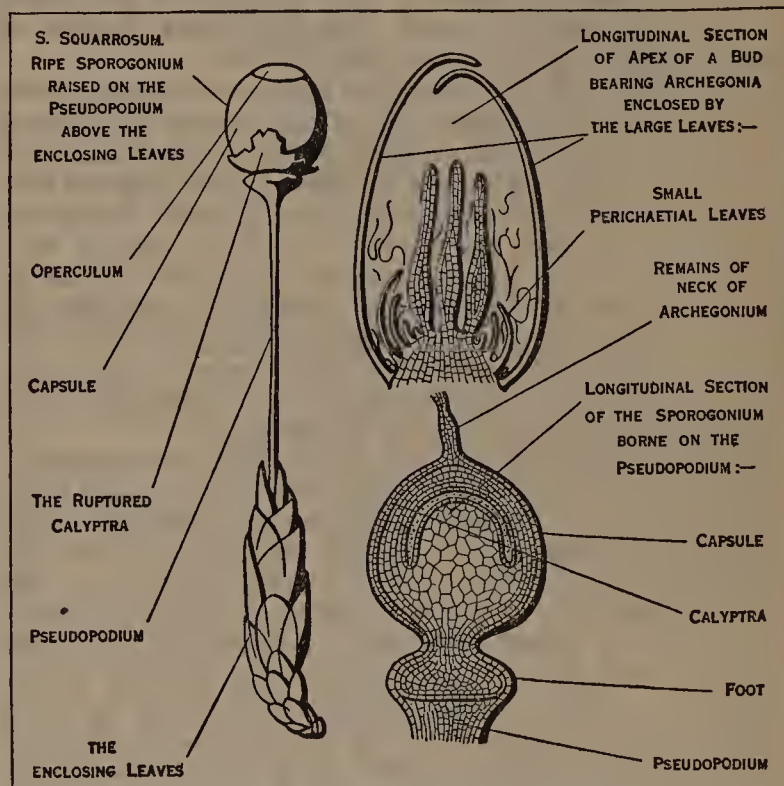
**Anthocerotales.**—The Anthocerotales, as mentioned previously, possess a simple thallus undifferentiated in either texture or habit, but are sharply separated from the remaining liverworts by reason of their sporogonium (fig. 8). There are very few genera in the group, the most noted being *Anthoceros*, *Dendroceros* and *Notothylas*. The thallus is dark green and its cells contain a single large chloroplast. On the under surface occur small slits filled with mucilage, which often also fills intercellular spaces in the thallus, and colonies of *Nostoc*, an alga, are constantly found inhabiting some of



FROM STRASBURGER, "TEXT-BOOK OF BOTANY"

FIG. 8.—*ANTHOCEROS LAEVIS*, A DARK GREEN LIVERWORT, ONE OF THE BEST KNOWN MEMBERS OF THE GROUP ANTHOCEROTALES

the mucilage slits. The group is specially noteworthy on account of its reproductive organs. Antheridia often occur in groups in chambers beneath the epidermis and are endogenous, in contrast to all other antheridia. The archegonia are superficial, but after fertilization become covered over by thallus growth and through this the sporogonium has to burst in its growth. The sporogonium



FROM GOEBEL, "PFLANZENMORPHOLOGIE," BY PERMISSION OF W. ENGELMANN

FIG. 9.—GENERAL STRUCTURE OF *SPHAGNUM ACUTIFOLIUM*, A PEAT MOSS, VERY ABSORBENT WHEN DRY, USED IN SURGICAL DRESSINGS

is a remarkable structure. It often reaches a length of an inch or more and consists of a wall several cells thick enclosing a spore sac and a sterile column of cells within, the columella. The spore sac overarches the columella, and besides spores, elaters of irregular shape are produced. The most peculiar feature, however, is that although there is no seta, a zone of tissue between the capsule and the foot remains actively growing and is adding new capsule tissues continuously from below during the life of the sporophyte. When mature, the capsule opens in two valves by splitting from the apex, and as spores are shed new ones are being added from



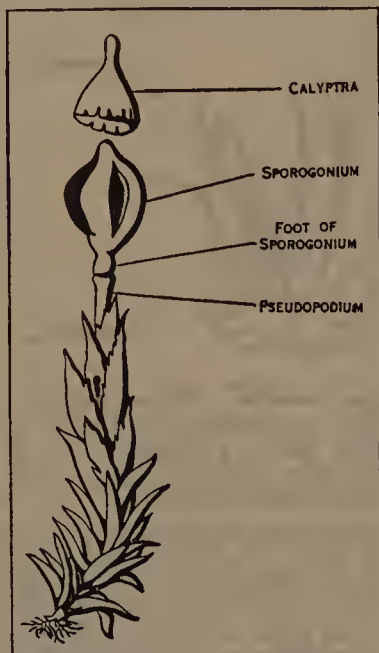
the base. Other features of interest are that the wall of the sporogonium contains stomata and chlorophyll and so can assimilate, and the foot buried in the thallus is irregular in outline. There are slight variations in details of structure between the few forms in this group, yet all are sufficiently peculiar in their structures to warrant the great interest they arouse.

### MUSCI

Musci or mosses, are on the whole more xerophytic (*i.e.*, suited to live under drier conditions) than liverworts and do not offer the same degree of variation in form and structure. All mosses consist of a distinct stem and leaves and almost all of them are radial in construction and not dorsiventral as are liverworts; in fact, apart from differences in smaller details all mosses are fundamentally the same in form (figs. 9, 10, 11). The stems have a single apical cell, the leaves, too, grow by a two-sided apical cell and do not show any trace of forking as was the case in the leafy liverworts. There is present the possibility of a good deal of differentiation in the tissues, for some mosses (*Polytrichum* for instance) reveal a structure almost analogous to the conducting strands of higher plants. The sexual organs, antheridia and archegonia, in mature form much like those of liverworts but differing in development, occur in groups at the apex of the main or lateral branches of the stem, with the exception of the antheridia of *Sphagnum*. They both occur in groups intermixed with peculiar hairs or paraphyses. The sporogonium developing from the fertilized egg has the usual capsule, stalk and foot, and is protected during its immature stages by the developing venter of the archegonium, the calyptra. As the sporogonium stalk elongates, the calyptra becomes torn, the upper half with the remains of the archegonium neck being carried up on top of the capsule, the lower half remaining as a frill round the base of the stalk. It is the sporogonium which at once clearly separates the mosses into three sub-groups, the Sphagnales and Andreaeales, both containing only a single genus, and the Bryales.

**Sphagnales.**—In the Sphagnales, with its single genus *Sphagnum*, the long stalk, the pseudopodium, bearing the capsule is not sporophytic but is a leafless prolongation of the axis of the gametophyte, embedded in the apex of which is the foot of the sporogonium (fig. 9). The seta is practically non-existent. The capsule consists of a wall a few cells thick enclosing a dome-shaped spore sac which overarches a sterile column of cells, the *columella*, which projects into the capsule from its base. Furthermore there is a lid or cap to the capsule, marked off by a ring of large cells, the *annulus*. This cap or *operculum* is thrown off at maturity by the activity of the cells of the annulus whereby the spore-sac is opened. There are no elaters in this or any other moss, and the spores in *Sphagnum* give rise to an unusual thalloid protonema. *Sphagnum* is a typical bog-forming moss and has leaves with very peculiar structure. These are one cell thick and consist of large, colourless empty cells open to the exterior by a pore, and surrounded by the comparatively small narrow chlorophyll-containing cells. The presence of these empty cells renders *Sphagnum* very absorbent, whence its use in surgical dressings.

In the Andreaeales, with its single genus *Andreaea* (fig. 10), again the sporogonium is borne aloft on a pseudopodium and the dome-shaped spore sac overarches the columella as in *Sphagnum*. Here, however, there is no operculum, the mature sporogonium opening by four slits down the side of the capsule.

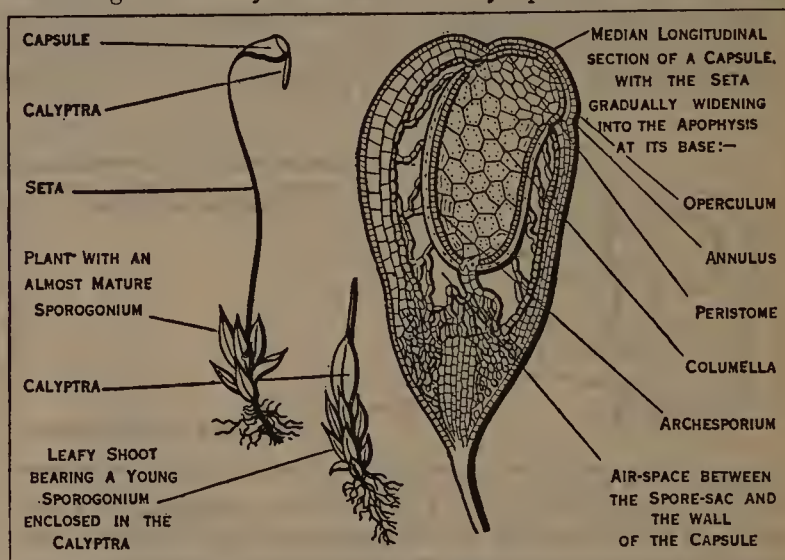


FROM STRASBURGER, "TEXT-BOOK OF BOTANY"  
FIG. 10.—ANDREAEA PETROPHILA, ONLY GENUS OF THE MOSS GROUP ANDREALES SHOWN BEARING AN OPEN CAPSULE

**Bryales.**—The Bryales afford the most complicated structure of the sporophyte. Here the capsule is, with very few exceptions, borne on a long seta at whose base, sunk in the apex of the stem of the gametophyte, is the foot. The capsule is remarkable in many respects (fig. 11). The wall is several cells thick, and there is a well-defined operculum delimited by an annulus. Within the capsule running from base to apex is a sterile column of cells, the columella, which is surrounded by the cylindrical spore sac. Surrounding the spore sac is an air chamber, the spore sac being connected with the wall by means of strands of cells or trabeculae. The wall of the capsule possesses stomata and its cells contain chlorophyll, so that the sporophyte here can assimilate to some extent. At the apex of the seta, adjoining the capsule, is a region highly developed in some forms (*Splachnum luteum*) which has abundant air spaces and stomata in its epidermis, a region known as the apophysis. More remarkable, however, is the *peristome* of the capsule. This consists of one or two layers of small teeth attached to the wall of the capsule just beneath the annulus at one end, but free elsewhere. When the capsule is mature and the operculum thrown off, these teeth close the now hollow spore-containing capsule when conditions are moist and so retain the spores, but curl back in dry weather and allow their discharge.

This structure of the sporogonium is fairly uniform throughout the Bryales with the exception of the condition seen in the Polytrichaceae where peristome teeth are not developed, the capsule when mature having a ring of pores in place of the peristome. It is not necessary to stress the obvious fact that in the Bryales sporogonium we have a very highly organized structure.

Space does not permit even mention of the many points of theoretical interest in the Bryophyta, or many unusual but interesting forms to be met with. These questions, with others which add to the interest of the group, may be followed in the literature cited. The Bryophyta play their part in questions of broader interest. A few, for instance, act as "colonisers," they can gain a foothold on bare rock or other uncongenial places where higher plants fail, and in this way in course of time prepare a suitable groundwork for these higher forms. Many mosses and liverworts are epiphytic on the stems or leaves of other plants and it is interesting that many of them are very specific in their choice



FROM GOEBEL, "PFLANZENMORPHOLOGIE"

FIG. 11.—FUNARIA HYGROMETRICA, A MEMBER OF THE BRYALES, A GROUP WHICH CONTAINS THE MAJORITY OF THE MOSS GENERA

of host. Therein lies an unsolved problem and there is need for careful recording of observations in this respect.

As to the origin of the Bryophyta as a whole, opinion is divided. We have little or no positive evidence from living or fossil forms, neither can we say definitely which of the higher groups of plants arose from them. Within themselves, as has been pointed out, they do show a serial progression, although instances of reduction are undoubtedly to be found. Such instances of reduction in structure have led some bryologists to look upon the simpler forms as derived from the higher by reduction, though this view is generally considered to be contrary to the mass of evidence. Between the Hepaticae, Anthocerotales, Sphagnales and Bryales



there are no connecting forms known, and it must be left as an open question whether Bryophyta are a monophyletic group or not. With regard to the relationship between Bryophyta and Pteridophyta the article on the latter group should be consulted. Although the alternating generations in the two are strictly comparable, no evidence of actual relationship is yet advanced.

For further information consult: Campbell, *Mosses and Ferns* (1895); Engler and Prantl, *Die natürlichen Pflanzenfamilien*, Teil I. Alt. 3 (Leipzig, 1909); Goebel, *Organography of Plants* (1900 and 1905); Cavers, "Inter-relationships of Bryophyta," *New Phytologist* (Reprint, Cambridge, 1911).

For identification of British species of liverworts and mosses:—Braithwaite, *British Moss Flora* (1887–1905); Pearson, *The Hepaticae of the British Isles* (1902); Dixon and Jameson, *The Student's Handbook of British Mosses* (1904); MacVicar, *The Student's Handbook of British Hepatics* (Eastbourne and London, 1926). (F. How.)

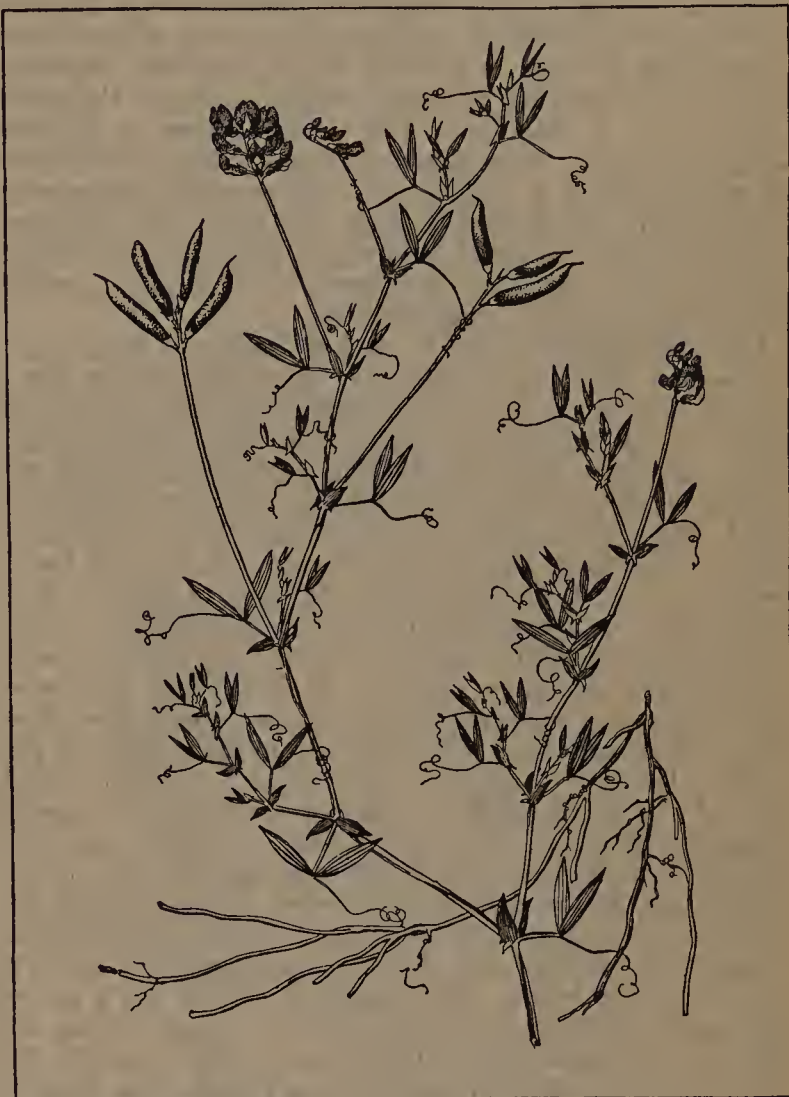
**LENTICEL**, a special organ, which appears as an elongated scar on the surface of the cells of trees, and which makes provision for gaseous interchange between the internal tissues and the external air after the formation of cork. A lenticel is formed by the phellogen dividing and giving rise to a loose tissue of rounded cells through which air can pass to the tissue below. The lenticels of the stem are usually found below the stomata whose function they take up after the latter have been cast off with the epidermis. See PLANTS.

**LEGUMINOSAE**, the second largest family of seed-plants, containing about 600 genera with 12,000 species. It belongs to the series Rosales of the Dicotyledons, and contains three well-marked subfamilies, Papilionatae, Mimosoideae and Caesalpinioidae. The plants are trees, shrubs or herbs of very various habit. The British representatives, all of which belong to the suborder Papilionatae, include a few shrubs, such as *Ulex* (gorse, furze), *Cytisus* (broom) and *Genista*, but the majority, and this applies to the suborder as a whole, are herbs, such as the clovers, *Medicago*, *Melilotus*, etc., sometimes climbing by aid of tendrils which are modified leaf-structures, as in *Lathyrus* and the vetches (*Vicia*). Scarlet runner (*Phaseolus multiflorus*) has a herbaceous twining stem. Woody climbers (lianes) are represented by species of *Bauhinia* (Caesalpinioidae),

which with their curiously flattened, twisted stems are characteristic features of tropical forests, and *Entada scandens* (Mimosoideae) also common in the tropics. These two suborders, which are confined to the warmer parts of the earth, consist chiefly of trees and shrubs such as *Acacia* and *Mimosa* belonging to the Mimosoideae, and the Judas tree of southern Europe (*Cercis*) and tamarind belonging to the Caesalpinioidae. The so-called acacia of European gardens (*Robinia Pseudacacia*) and laburnum are examples of the tree habit in the Papilionatae. Water plants are rare, but are represented by *Aeschynomene* and *Neptunia*, tropical genera. The roots of many species bear nodular swellings (tubercles), the cells of which contain bacterium-like bodies which have the power of fixing the nitrogen of the atmosphere. Hence the value of these plants as a crop on poor soil or as a member of a series of rotation of crops, since they enrich the soil by the nitrogen liberated by the decay of their roots.

**Leaf Forms.**—The leaves are alternate in arrangement and generally compound and stipulate. A common form is shown by the clovers, which have three leaflets springing from a common point (digitately trifoliate); pinnate leaves are also frequent as in laburnum and *Robinia*. In Mimosoideae the leaves are generally bipinnate. Rarely are the leaves simple as in *Bauhinia*.

Various departures from the usual leaf-type occur in association with adaptations to different functions or environments. In leaf-climbers, such as pea or vetch, the end of the rachis and one or more pairs of leaflets are changed into tendrils. In gorse the leaf is reduced to a slender, spine-like structure, though the leaves of the seedling have one to three leaflets. In many Australian acacias the leaf surface in the adult plant is much reduced, the petiole be-



FROM CURTIS, "FLORA LONDINIENSIS"

FIG. 2.—MEADOW VETCHLING (*LATHYRUS PRATENSIS*)

ing at the same time flattened and enlarged, and frequently the leaf is reduced to a petiole flattened in the vertical plane; by this means a minimum surface is exposed to the intense sunlight. In the garden pea the stipules are large and foliaceous, replacing the leaflets, which are tendrils; in *Robinia* the stipules are spiny and persist after leaf-fall. In some acacias (*q.v.*) the thorns are hollow, and inhabited by ants as in *A. sphaerocephala*, a Central American plant, and various others. In some species of *Astragalus*, *Onobrychis* and others, the leaf-stalk persists after the fall of the leaf and becomes hard and spiny.

Leaf-movements occur in many of the genera. Such are the sleep-movement in the clovers, runner bean (*Phaseolus*), *Robinia* and *Acacia*, where the leaflets assume a vertical position at night-fall. Spontaneous movements are exemplified in the telegraph-plant (*Desmodium gyrans*), native of tropical Asia, where the small lateral leaflets move up and down every few minutes. The sensitive plant (*Mimosa pudica*) is an example of movement in response to contact, the leaves assuming a sleep-position if touched. The seat of the movement is the swollen base of the leaf-stalk, the so-called pulvinus.

**Flowers and Fruit.**—The flowers occur in simple clusters, such as the simple raceme (*Laburnum*, *Robinia*), which is condensed to a head in *Trifolium*; in *Acacia* and *Mimosa* the flowers are densely crowded. The flower is characterized by a hypogynous or slightly perigynous arrangement of parts, the anterior position of the odd sepal, the free petals, and the single median carpel with a terminal style, simple stigma and two alternating rows of ovules



AFTER DR. FLEMING, BY COURTESY OF THE TRUSTEES OF THE BRITISH MUSEUM (NATURAL HISTORY)

FIG. 1.—BABUL (*ACACIA ARABICA*)



on the ventral suture of the ovary which faces the back of the flower.

The arrangement of the petals and the number and cohesion of the stamens vary in the three suborders. In Mimosoideae, the smallest of the three, the flower is regular, and the sepals and petals have a valvate aestivation, and are generally pentamerous, but 3-6-merous flowers also occur. The sepals are more or less united into a cup, and the petals sometimes cohere at the base. The stamens vary widely in number and cohesion; in *Acacia* they are indefinite and free, in the tribe *Ingeae*, indefinite and monadelphous, in other tribes as many or twice as many as the petals. Frequently, as in *Mimosa*, the long yellow stamens are the most conspicuous feature of the flower. In Caesalpinoideae the flowers are zygomorphic in a median plane and generally pentamerous. The sepals are free, or the two upper ones united as in tamarind, and imbricate in aestivation, rarely as in the Judas tree, valvate. The corolla shows great variety in form; it is imbricate in aestivation, the posterior petal being innermost.

The stamens, generally ten in number, are free, as in *Cercis*, or more or less united, as in *Amherstia*, where the posterior one is free and the rest are united. In tamarind only three stamens are fertile. The largest suborder, Papilionatae, has a flower zygomorphic in the median plane. The five sepals are generally united, and have an ascending imbricate arrangement; the calyx is often two-lipped. The corolla has five unequal petals with a descending imbricate arrangement; the upper and largest, the standard (*vexillum*), stands erect, the lateral pair, the wings or *alae*, are long-clawed, while the anterior pair cohere to form the keel or *carina*, in which are enclosed the stamens and pistil. The ten stamens are monadelphous, as in gorse or broom, or diadelphous, as in sweet pea (the posterior one being free), or almost or quite free; these differences are associated with differences in the methods of pollination. The ten stamens here, as in the last suborder, though arranged in a single whorl, arise in two series, the five opposite the sepals arising first. The carpel is sometimes stalked and often surrounded at the base by a honey-secreting disk; the style is terminal and in the zygomorphic flowers is often curved and somewhat flattened with a definite back and front. Sometimes as in species of *Trifolium* and *Medicago* the ovules are reduced to one. The pod or legume splits along both sutures into a pair of membranous, leathery or sometimes fleshy valves, bearing the seeds on the ventral suture. Dehiscence is often explosive, the valves separating elastically and twisting spirally, thus shooting out the seeds, as in gorse, broom and others. In *Desmodium*, *Entada* and others the pod is constricted between each seed, and breaks up into indehiscent one-seeded parts; it is then called a lomentum; in *Astragalus* it is divided by a longitudinal septum.

The pods show a very great variety in form and size. Thus in the clovers they are a small fraction of an inch, while in the common tropical climber *Entada scandens* they are woody structures more than a yard long and several inches wide. They are generally more or less flattened, but sometimes round and rod-like, as in species of *Cassia*, or are spirally coiled as in *Medicago*. In *Colutea*, the bladder-senna of gardens, the pod forms an inflated bladder which bursts under pressure; it often becomes detached and is blown some distance before bursting. In some cases the hard seed-coat itself is bright-coloured as in the scarlet seeds of *Abrus precatorius*, the so-called weather-plant. In the ground-nut (*Arachis hypogaea*), *Trifolium subterraneum* and others, the flower-stalks grow downwards after fertilization of the ovules and bury the fruit in the earth. In the suborders Mimosoideae and Papilionatae the embryo fills the seed or a small quantity of endosperm occurs, chiefly round the radicle. In Caesalpinoideae endosperm is absent, or present forming a thin layer round the embryo as in the tribe *Bauhinieae*, or copious and cartilaginous as in the *Cassieae*. The embryo has generally flat leaf-like or fleshy cotyledons with a short radicle.

Insects play an important part in the pollination of the flowers. In the two smaller suborders the stamens and stigma are freely exposed and the conspicuous coloured stamens serve as well as the petals to attract insects; in *Mimosa* and *Acacia* the flowers are crowded in conspicuous heads or spikes. The relation of insects

to the flower has been carefully studied in the Papilionatae, chiefly in European species. Where honey is present it is secreted on the inside of the base of the stamens and accumulated in the base of the tube formed by the united filaments round the ovary. It is accessible only to insects with long probosces, such as bees. In these cases the posterior stamen is free, allowing access to the honey. The flowers stand more or less horizontally; the large, erect, white or coloured standard renders them conspicuous, the wings form a platform on which the insect rests and the keel encloses the stamens and pistil, protecting them from rain and the attacks of unbidden pollen-eating insects. In his book on the fertilization of flowers, Hermann Müller distinguishes four types of papilionaceous flowers according to the way in which the pollen is applied to the bee (see POLLINATION).

**Distribution.**—The family is cosmopolitan, and often forms a characteristic feature of the vegetation. Mimosoideae and Caesalpinoideae are richly developed in the tropical rain forests, where Papilionoideae are less conspicuous and mostly herbaceous; in sub-tropical forests arborescent forms of all three suborders occur. In the temperate regions, tree-forms are rare—thus Mimosoideae are unrepresented in Europe; Caesalpinoideae are represented by species of *Cercis*, *Gymnocladus* and *Gleditschia*; Papilionoideae by *Robinia*; but herbaceous Papilionatae abound and penetrate to the limit of growth of seed-plants in arctic and high alpine regions. Shrubs and under-shrubs, such as *Ulex*, *Genista*, *Cytisus*, are a characteristic feature in Europe and the Mediterranean area. Acacias are an important component of the evergreen bush-vegetation of Australia, together with genera of the tribe *Podalyrieae* of Papilionatae (*Chorizema*, *Oxylobium*, etc.). *Astragalus*, *Oxytropis*, *Hedysarum*, *Onobrychis* and others are characteristic of the steppe-formations of eastern Europe and western Asia.

The suborder Papilionatae of the family is well represented in Great Britain. Thus *Genista tinctoria* is dyers' greenweed, yielding a yellow dye; *G. anglica* is needle furze; other shrubs are *Ulex* (*U. europaeus*, gorse, furze or whin, *U. nanus*, a dwarf species) and *Cytisus scoparius*, broom. Herbaceous plants are *Ononis spinosa* (rest-harrow), *Medicago* (medick), *Melilotus* (melilot), *Trifolium* (the clovers), *Anthyllis vulneraria* (kidney-vetch), *Lotus corniculatus* (bird's-foot trefoil), *Astragalus* (milk-vetch), *Vicia* (vetch, tare) and *Lathyrus*.

The most representative genera in the United States are as follows: *Baptisia* (false indigo), *Crotalaria* (rattlebox), *Lupinus* (lupine), *Trifolium* (clover), *Petalostemon* (prairie clover), *Robinia* (locust), *Astragalus* (milk vetch), *Desmodium* (tick trefoil), *Lespedeza* (bush clover), *Vicia* (vetch), *Lathyrus* (everlasting pea), *Gymnocladus* (Kentucky coffeetree), *Gleditsia* (honey locust), *Cassia* (senna), *Cercis* (redbud), *Mimosa* and *Acacia*. The conspicuous genus in the western United States is *Astragalus*, represented by about 275 species.

**Economic Importance.**—The family is of great economic value, containing many plants that are widely cultivated. The seeds, which are rich in starch and proteins, form valuable foods, as in pea, the various beans, vetch, lentil, ground-nut (*Arachis*) and others; seeds of *Arachis* and others yield oils; those of *Physostigma venenosum*, the Calabar ordeal bean, contain a strong poison. Many are useful fodder-plants, as the clovers (*Trifolium*) (*q.v.*), *Medicago* (e.g., *M. sativa*, lucerne [*q.v.*], or alfalfa); *Melilotus*, *Vicia*, *Onobrychis* (*O. sativa* is sainfoin, *q.v.*); species of *Trifolium*, lupine and others are used as green manure. Many of the tropical trees afford useful timber; *Crotalaria*, *Sesbania*, *Aeschynomene* and others yield fibre; species of *Acacia* and *Astragalus* yield gum; *Copaifera*, *Hymenaea* and others balsams and resins; dyes are obtained from *Genista* (yellow), *Indigofera* (blue) and others (*Haematoxylon campechianum* is logwood); of medicinal value are species of *Cassia* (senna leaves) and *Astragalus*; *Tamarindus indica* is tamarind, *Glycyrrhiza glabra* yields liquorice root. Well-known ornamental trees and shrubs are *Cercis* (*C. Siliquastrum* is the Judas tree), *Gleditschia*, *Genista*, *Cytisus* (broom), *Colutea* (*C. arborescens* is bladder-senna), *Robinia* and *Acacia*; *Wistaria sinensis*, a native of China, is a well-known climbing shrub; *Phaseolus multiflorus* is the scarlet runner; *Lathyrus*



(sweet and everlasting peas), *Lupinus*, *Galega* (goat's-rue) and others are herbaceous garden plants. *Ceratonia Siliqua* is the carob-tree of the Mediterranean, the pods of which (algaroba or St. John's bread) contain a sweet juicy pulp and are largely used for feeding live stock.

**BORAGINACEAE**, a family of plants belonging to the sympetalous section of dicotyledons, and a member of the series Tubiflorae. They are rough-haired annual or perennial herbs,



FROM THEDENIUS, "SKOLBOTANIK" BY PERMISSION OF IVAR HAEGGSTROMS BOKTRYCKERI AND BOKFORLAGS

THE FORGET-ME-NOT (*MYOSOTIS PALUSTRIS*) A MEMBER OF THE BORAGINACEAE FAMILY LONG REGARDED AS AN EMBLEM OF FRIENDSHIP

more rarely shrubby or arborescent in tropical and sub-tropical forms. The leaves, generally alternate, are usually entire and narrow. The radical leaves in some genera, as *Pulmonaria* (lungwort) *Cynoglossum*, differ from the stem-leaves, being broader and sometimes heart-shaped. A characteristic feature is the one-sided (*dorsiventral*) inflorescence, illustrated in forget-me-not (*Myosotis*); the cyme is at first closely coiled, becoming uncoiled as the flowers open. Often the flowers are red in bud, becoming blue as they expand, as in *Myosotis*. The flowers are generally regular; the form of the corolla is rotate in borage, tubular in comfrey, funnel-shaped in hound's-tongue. The throat is often closed by scale-like outgrowths from the corolla, forming the corona.

The five stamens alternate with the lobes of the corolla. The ovary, of two carpels, is seated on a ring-like disc which secretes honey. Each carpel becomes divided by a median constriction each containing one ovule; the style springs from the centre. The colour of the flowers and the presence of honey serve to attract insects. The scales around the throat of the corolla protect it from wet or undesirable visitors, and by difference in colour from the corolla-lobes, as in the yellow eye of forget-me-not, may serve to indicate the position of the

honey. In most genera the fruit is a one-seeded nutlet; there are generally four, but one or more may not develop.

The family is widely spread in temperate and tropical regions, and contains 100 genera with about 1,000 species. Its chief centre is the Mediterranean region, whence it extends over central Europe and Asia, becoming less frequent northwards. A smaller centre occurs on the Pacific side of North America. The family is less developed in the south temperate zone. It is of little economic value. Several genera, such as borage, were formerly used in medicine, and the roots yield purple or brown dyes. Heliotrope or cherry-pie (*Heliotropium peruvianum*) is a well-known garden plant.

In Great Britain the family is represented by some 12 genera and upwards of 25 species; among these are the borage (*Borago officinalis*), the gromwell (*Lithospermum officinale*), the hound's-tongue (*Cynoglossum officinale*), the viper's-bugloss (*Echium vulgare*) and several species of forget-me-not or scorpion-grass (*Myosotis*). In North America there are about 30 genera and upwards of 250 species, most numerous in the western United States. In the northeastern States and adjacent Canada about 50 species are found, one-third of which are naturalized; in the Rocky Mountain region upwards of 150 species occur; in the Great Basin (Utah and Nevada) there are more than 100 species, and in California, more than 90. Exclusively North American genera

are *Allocarya*, *Amsinckia*, *Cryptantha*, *Oreocarya* and *Plagiobothrys*.

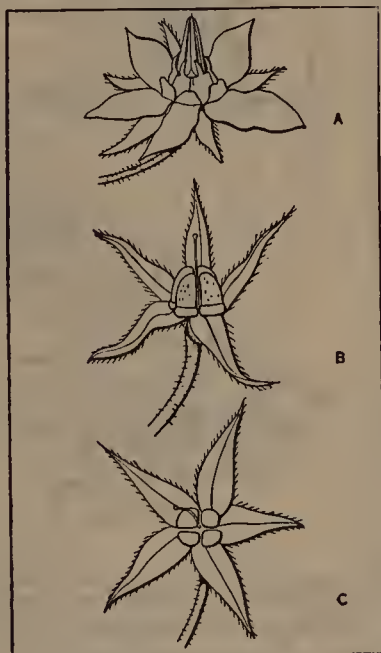
**TRUNK** (Fr. *tronc*, Lat. *truncus*, cut off, maimed), properly the main stem of a tree from which the branches spring, especially the stem when stripped of the branches.

**PERENNIALS**, the name given to those plants whose natural term of life or life cycle continues for more than two growing periods or years in contradistinction to annuals (*q.v.*), which exist for a single growing period, and biennials (*q.v.*) whose life term embraces only two growing periods. Perennials may be woody (*e.g.*, trees and shrubs) or herbaceous (*e.g.*, iris).

**PTERIDOPHYTA**, one of the groups comprising the ferns and their allies, of the second great division of plants, the Archegoniatae, the other being the Bryophyta (*q.v.*). The Pteridophyta thus share with the Bryophyta a middle position between the essentially aquatic Thallophytes and the essentially terrestrial Spermatophytes. Much of their special interest centres round that fact. They include plants well represented at the present day; but many already existed in the early land-vegetation of the Devonian period, now known only as fossils; they appeared in greater profusion as fossils of the coal, and many of these early types continued on into the Mesozoic age while their correlatives are included in the flora of the present day. Thus their geological history supports the conclusion that they take a middle position in the evolutionary progression of plant-life, in which a transition from life in water to life on land was a striking incident.

VIPER'S-BUGLOSS (*ECHIUM VULGARE*) SOMETIMES CALLED THE BLUE THISTLE

A biennial plant common to grain-fields, it owes its name to stem spots which resemble the marks on a viper



FROM STRASBURGER, "TEXTBOOK OF BOTANY" (MACMILLAN & CO.)

BORAGE (*BORAGO OFFICINALIS*), SHOWING CHARACTERISTIC STRUCTURE AND HAIRINESS OF FLOWER  
A. Flower; B. and C. Fruit

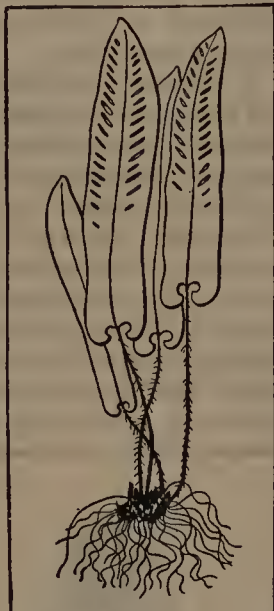
Hofmeister first showed that there is essential similarity underlying the life-histories of mosses and ferns, and that the same scheme, in modified form, extends to the seed-plants also. Since this is so, an account of the Pteridophyta may fitly be introduced by a brief record of the life-history of a fern, as an example of the Archegoniatae generally, and of the Pteridophyta in particular. There are two periods in each normally completed life-cycle of these plants when the individual is represented by a single cell; and these punctuate the limits between two distinct bodily phases



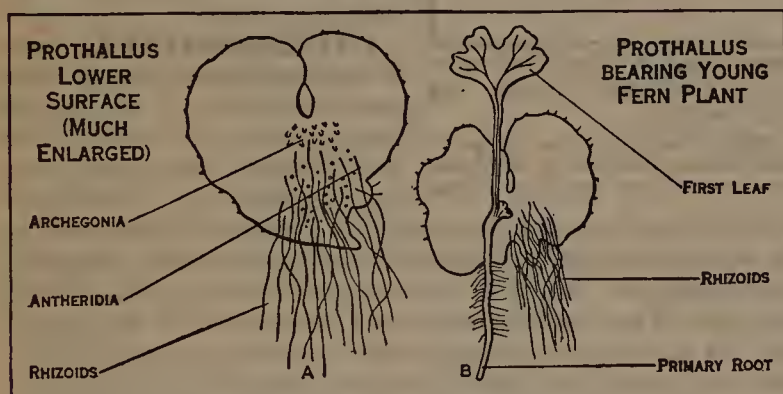
or generations as they are called. One of these is the leafy *fern plant* which every one knows; the other is a small green scale-like body, delicate in texture, called the *prothallus*, which escapes the observation of most people, though actually common enough. The former is sexless, but bears *spores* in large numbers; it is the *sporophyte* generation. The latter is the sexual generation, and, since it produces *gametes*, it is called the *gametophyte*.

**Life-history of a Fern.**—The fern plant varies in size from a minute herb to a tree-like body, 60 or even 80 ft. in height. It consists of a stem bearing characteristic leaves, usually of large size and delicate outline; the shoot thus constituted is attached by roots to the soil, the whole being traversed by conducting tracts. Since the green leaves serve a nutritional function, the plant is able to subsist as a perennial land-plant (fig. 1). On the leaves the *sori* are borne, of various form and position. In the hart's tongue or the common shield fern they appear as dense groups of brown *sporangia* seated on the lower surface, and covered while young by a membranous *indusium*. Each sporangium is a stalked capsule containing numerous minute, dry and dusty spores, which are violently ejected when ripe, and each is then liable to be carried away individually by the breeze. The spores are unicellular propagative organs.

Each spore germinating on moist soil may grow into a prothallus or gametophyte (fig. 2), which never grows large, though being green it is physiologically independent. It bears the *sexual organs* or *gametangia*, usually on its lower surface (fig. 2, A). Near its base are the male gametangia or *antheridia*, which when ripe consist each of a protective wall of cells surrounding numerous spermatoocytes. When bathed by external water (rain or dew) the wall ruptures, and each spermatoocyte emits a single spiral *spermatozoid*, which moves in the water by lashing cilia (fig. 3). Near the indented apex of the prothallus the female gametangia or *archegonia* are formed (fig. 2). They are flask-shaped organs, also protected by an external wall; each contains a row of three



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)  
FIG. 1.—HART'S TONGUE (PHYLITIS SCOLOPENDRIUM)

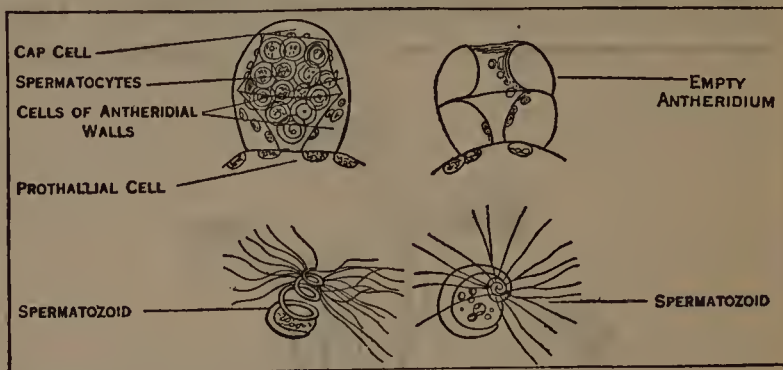


FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)  
FIG. 2.—PROTHALLUS OF SHIELD FERN (DRYOPTERIS FILIX MAS)

cells, of which the lowest and largest is the ovum or egg, sunk in the tissue of the parent (fig. 4). When ripe the archegonium also ruptures on access to external water, the distal cells of the wall parting so that an open channel filled with mucilage leads down to the rounded egg. *Fertilization (syngamy)* consists in the fusion of the spermatozoid with the egg to which it is attracted by soluble substance diffusing from it into the water that bathes the open archegonium. The result of that fusion is the *zygote*, which is the starting point for the development of a new fern plant. This new individual appears first as a spherical mass of delicate cells, nursed in the cavity of the archegonium; but it soon bursts out with its first leaf and root, and its apical bud ready to grow into a new fern, while the prothallus rots

away (fig. 2, B).

The central feature in syngamy is the *coalescence of the male and female nuclei*; the resulting fusion-nucleus is then *diploid*, with the  $2x$  number of chromosomes (see CYTOLOGY). That character is then maintained throughout the tissues of the sporophyte. On the other hand, when the fern-plant comes to maturity and forms sporangia, the cells that are to form the spores undergo

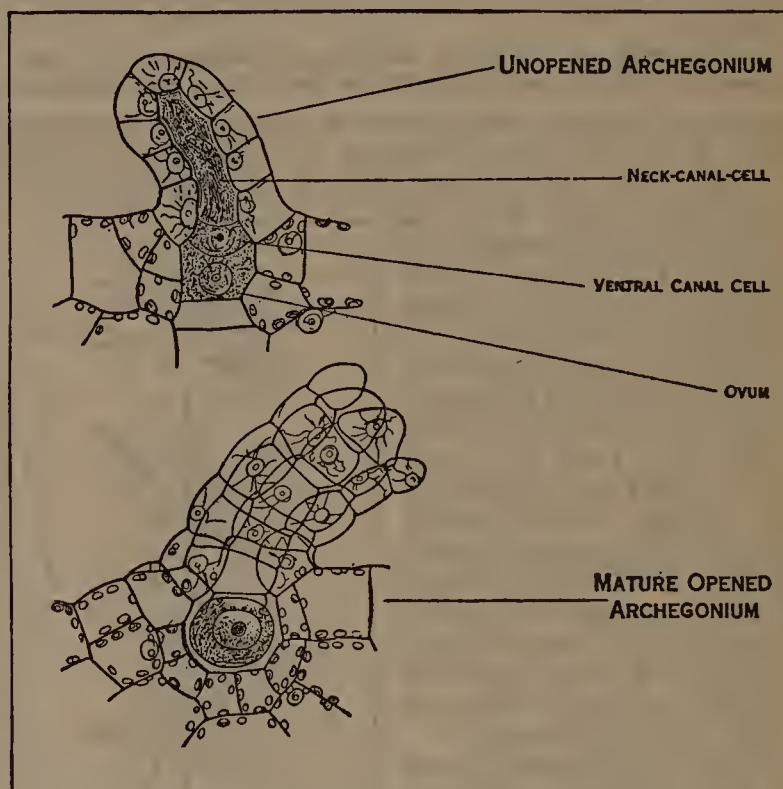


FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 3.—ANTHERIDIUM OF POLYPODY (POLYPODIUM VULGARE)

a nuclear change, called *reduction* or *meiosis*, by which they resume that simpler constitution possessed by the nuclei of the prothallus, and described as *haploid* ( $x$ ). These events normally alternate in regular succession, and they constitute that *nuclear cycle* which underlies all normal life-histories of the Archegoniatae. They stamp structurally the distinction of the two alternating generations. Such alternation, in one form or another, appears in all plants that show sexuality.

The Pteridophyta illustrate the cytological cycle with unusual clearness, since the two somatic phases (viz., the haploid prothallus and the diploid fern plant) are so unlike, and so markedly independent the one of the other during their adult existence. It seems probable that in the course of evolution some simple



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 4.—ARCHEGONIUM OF POLYPODY (POLYPODIUM VULGARE)

form of alternation present in an algal ancestry has been regularized and standardized in the Archegoniatae in accordance with a passage from the relative uniformity of aquatic life to the more varied vicissitudes of life on land. In the Bryophyta the gametophyte was more adaptive, and became the dominant generation; on the other hand, in the Pteridophytes, as also in all the higher land-plants, the sporophyte became specialized as the dominant land-living organism. But the Archegoniatae themselves were never wholly emancipated from dependence on external liquid water. They show their amphibious character by



their zoidiogamic fertilization; and this confirms their position as primitive land-plants.'

For the most part the Pteridophyta are like the Bryophyta in possessing only one type of spore (*homosporous*); but they produce these in enormous numbers. A common shield fern may ripen over 50 millions of them in a season. This is a primitive mode of propagation characteristic of early vegetation.

On the other hand, some few Pteridophyte-types such as *Selaginella* and *Isoetes*, and those curious little fern-derivatives styled collectively the Hydropterideae, possess sexually-differentiated spores, and are described as *heterosporous*; numerous smaller spores (*microspores*) bear each a rudimentary male prothallus, while a few larger spores (*megaspores*), or only a single one, produce each a massive female prothallus. In this they show a state of specialized advance along lines that have led to the final success of the flowering plants. The Pteridophytes as a whole present the paradox of a great division of the vegetable kingdom that has achieved success by force of numbers, rather than by the more refined methods of physiological adjustment and of propagation even in the higher plants.

These paragraphs, of necessity rather technical, will suffice to introduce the Pteridophyta, Vascular Cryptogams, or fern-allies as they are sometimes called. They are represented by six natural groups or classes of organisms, of which four include forms both living and fossil, but two are known only as extinct and very early fossils. Such facts at once confirm their position as representing a primitive vegetation. They may be arranged in rough sequence according to their complexity of form and structure; but this must not be understood as conveying any definite view as to affinity.

## CLASSIFICATION

I. PSILOPHYTALES, comprising only fossil types of simple conformation, from early Devonian rocks.

II. PSILOTALES, represented by two genera of living plants, *Psilotum* which is intertropical, and *Tmesipteris* which is confined to Australia.

III. SPHENOPHYLLALES, containing extinct Palaeozoic fossils of small size, which hardly extended into the Mesozoic period.

IV. EQUISETALES, including only the single living genus of the horsetails (*Equisetum*), but largely represented also by Palaeozoic fossils often of dendroid form (Calamariaceae).

V. LYCOPODIALES, or so-called club-mosses, well represented at the present day by the large genera, *Lycopodium* and *Selaginella*; also by *Phylloglossum* and *Isoetes*. But in the Palaeozoic period there existed the giant Lepidodendroid trees, as well as allied plants of humbler dimensions.

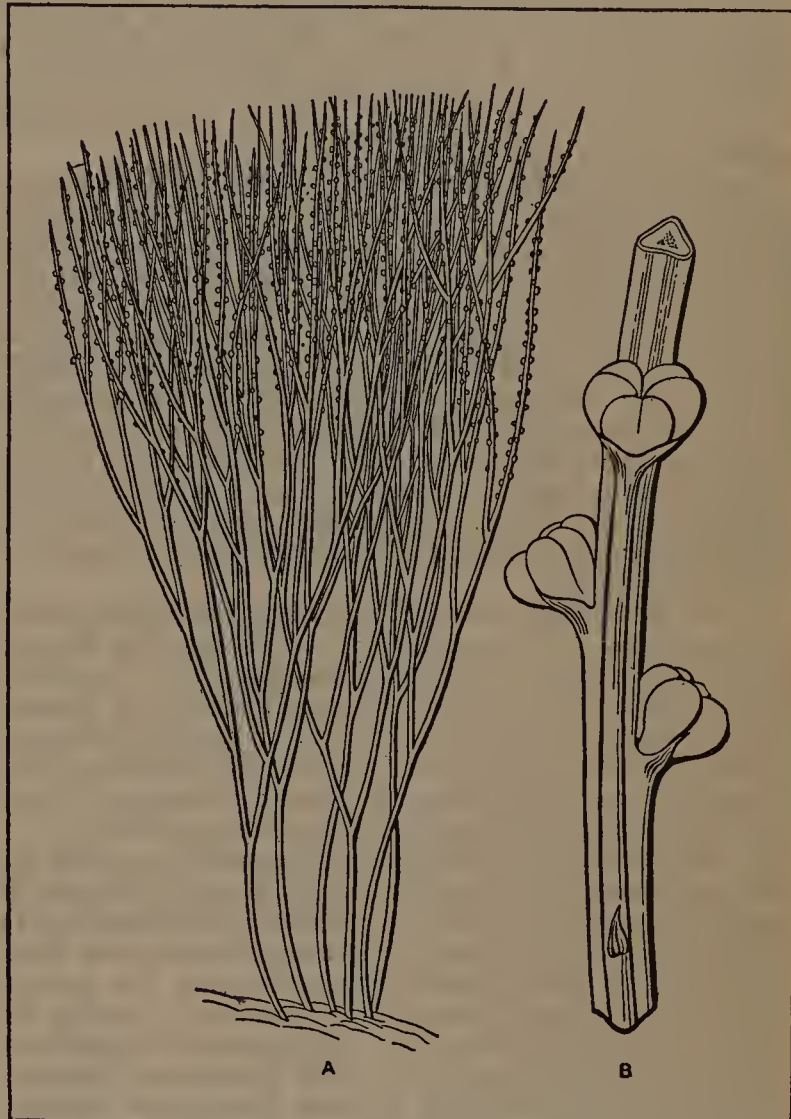
VI. FILICALES, or ferns; these comprise not only the living ferns, with about 150 genera and over 6,000 species, but also a rich sequence of fossils, from the Palaeozoic Coenopteridaceae to the most recent strata.

I. **Psilophytales.**—This new class of plants was constituted by Kidston and Lang to receive certain fossils of early Devonian time, discovered by Dr. Mackie at Rhynie in Aberdeenshire. Its name is taken from the old genus *Psilophyton* of Dawson, and the class now comprises a number of other genera of like age, more recently discovered, forming together a very distinctive

flora. But of these only the sporophyte is known (fig. 5). The vegetative system consists of upward-growing, forked, aerial shoots that spring from a rhizome sometimes creeping, sometimes tuberous and mycorrhizic; sometimes the underground branchlets are root-like, forking in the substratum (*Asteroxylon*). The erect shoots are cylindrical, and were evidently green, covered by an epidermis, with stomata, and they are traversed by conducting strands of simple structure. Various superficial growths, often with the ap-

pearance of thorns or prickles, are borne upon the larger branches, as in *Psilophyton* and *Asteroxylon*. The plants were of low stature, and growing gregariously they must have looked rather like grass. The genera *Hornea*, *Rhynia* and *Asteroxylon*, described by Kidston and Lang were so well preserved that their structure is as well known as though they were modern plants. The class stands conspicuously apart as leafless and rootless vascular plants.

The most distinctive feature of the class for diagnosis is that



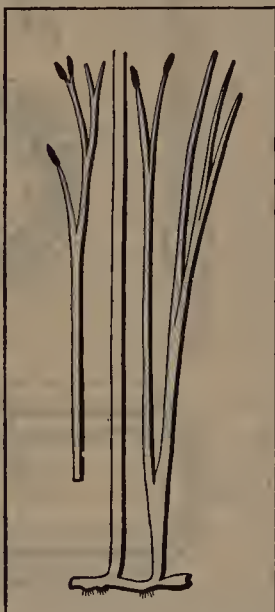
FROM ENGLER & PRANTL, "DIE NATÜRLICHEN PFLANZENFAMILIEN" (WILHELM ENGELMANN)  
FIG. 6.—PSILOTUM TRIQUETRUM. (A) HABIT OF PLANT, SHOWING DICHOTOMOUS BRANCHING (B) PART OF A SHOOT

the large sporangia, protected by a wall of many layers and containing numerous homosporous spores, are terminal on the vegetative twigs.

The very early existence thus demonstrated of leafless, and rootless and homosporous vascular plants, with distal sporangia of primitive construction is a fact of the first comparative importance. It is true it does not demonstrate any nearer connection with the Algae, but as regards other relations the new facts are highly suggestive. Long ago it was remarked that the widest gap in the sequence of plants was that between the Bryophytes and Pteridophytes. It is within this gap that the newly discovered fossils take their natural place, acting as synthetic links for the whole sequence of land-living, sporangium-bearing plants.

II. **Psilotales.**—Whereas the Psilophytales are known only by their fossil sporophytes, the Psilotales are represented by two living genera, *Psilotum* and *Tmesipteris*, of which both generations are now known. They form a natural family of the Psilotaceae. By their features they appear remarkably isolated among living plants, and their nearest affinity is to be sought among the Psilophytales and Sphenophyllales, both being classes of plants long extinct. These two genera appear in fact as living fossils.

They live epiphytically, or in soil rich in humus, and are rootless. The green, more or less shrubby shoot is fixed in the substratum by much branched leafless rhizomes, which are infected



FROM KIDSTON & LANG IN BOWER, "FERNS" (CAMBRIDGE UNIVERSITY PRESS)

FIG. 5.—HORNEA LIGNIERI



by a mycorrhizic fungus. The saprophytic nutrition by these is supplemented by photosynthesis in the green leafy shoots. In *Psilotum* the aerial stems bifurcate, bearing small and simple scaly leaves, which however pass upwards into bifid "sporophylls," and between the two teeth is seated a large trilocular synangium, containing numerous homosporous spores (fig. 6). *Tmesipteris* resembles it in general character, but branching is infrequent, the leaves and "sporophylls" are larger, and the synangium has only two large loculi. The anatomy of the green stem of *Psilotum*, with its epidermis and stomata, its photosynthetic cortex and conducting protostele, is on the same general plan as that of *Rhynia* or *Asteroxylon*; the bifurcation and presence of minute leaves, and the rootless mycorrhizic base all support the comparison with the Devonian types of Rhynie.

The prothalli of both genera have been discovered since 1914. They are colourless, nourishing themselves saprophytically through fungal agency. In fact these primitive plants conform in their life-cycle to what is seen in many primitive ferns and Lycopods. Moreover, the embryology has been traced in *Tmesipteris*; there is neither suspensor, nor root, nor cotyledon. The embryo with its apex directed, like that of the Bryophytes towards the neck of the archegonium, soon bursts its way out, proceeding to branch distally and form a leafless rhizomic system from which aerial shoots arise later. Such details of the gametophyte link the Psilotales, and indirectly the Psilophytales, with other Pteridophytes as regards alternation on the whole; but the rootless and leafless embryo presents a state that finds its nearest comparison with the Bryophyta.

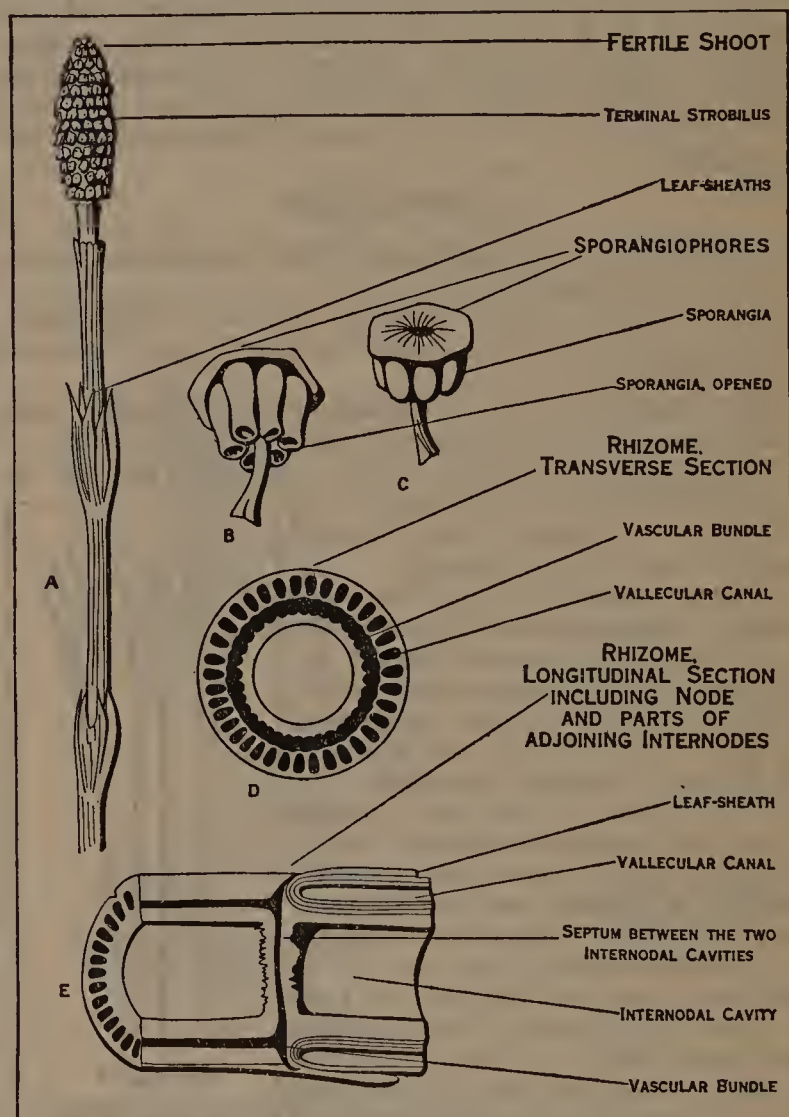
**III. Sphenophyllales.**—The two genera *Sphenophyllum* and *Cheirostrobus* are the representatives of this class, but in more or less loose association with them are such types as *Pseudobornia* and *Hyenia*; these suggest that the articulate type of land-plants, which they all illustrate, in common with the horsetails, was well represented in the primary rocks. The existence of the Sphenophyllales extended from the Upper Devonian to Triassic time. (For details of Sphenophyllales see PALAEOBOTANY.)

**IV. Equisetales.**—Those Pteridophyta which have their appendages disposed in successive whorls, with long internodes intervening between them, have been designated the Articulatae. In the distant past this type was strongly represented by the Sphenophyllales, and by the Calamariaceae and others. But it is familiar to us to-day as it is seen in the horsetails, included in the cosmopolitan genus *Equisetum*, the only species of Equisetaceae, and the only living representatives of the Equisetales. These are semi-aquatic plants; they vary in height from a few inches to 30 ft. or more, and are rhizomatous, with erect shoots arising from richly branched, subterranean stems, which are themselves rooted in the soil. The habit of the plants depends upon the method of branching of the shoot rather than upon the foliage, for the leaves are minute (microphyllous), and closely appressed to the stem that bears them. Each whorl of them forms a sheath closely investing the base of the next higher internode, while the teeth projecting upwards from it are all that represent the individual leaves. Their position alternates in successive nodes (fig. 7). The internodes are fluted, the ridges being continuous downwards from the next higher leaves; consequently those of successive internodes alternate. The number of the leaves in a whorl may vary according to the size of the stem, from three to 20 or 30. This is the scheme of the shoot in all species of *Equisetum*, and the shoot is constantly of radial construction. In some species the branching is sparse (*E. limosum*); in others it is profuse (*E. sylvaticum* and *maximum*), and the branches may themselves branch again repeatedly. Their number and the degree of secondary branching defines the habit, and justifies for the more bushy types the familiar name of horsetails. The branches arise in the axils of the leaf-sheaths, but they alternate with the leaves themselves. Many of those initiated remain dormant. A root is found at the base of each bud, but it also is frequently dormant, especially in aerial shoots. The structure of the underground rhizome is on the same plan as that of the aerial branches that it bears. Thus the whole plant consists of a succession of shoots, each with a dominant axis, whorls of subordinate leaves, and

accessory roots.

In the transverse section of an aerial internode the sinuous outline shows the projecting ridges and depressed furrows of its fluted form, though this is less evident in the rhizomes (fig. 7, D). The centre of the section is occupied by a large air-cavity, surrounded by the remains of the pith. A circle of isolated vascular strands, corresponding in number to the leaves in the next whorl above, is in most species enclosed by a sinuous endodermis, which thus delimits the stele (*E. arvense*, etc.). Outside this lies the cortex, marked by an equal number of large air-cavities, which alternate with the vascular strands, and correspond to the furrows of the fluting. The vascular strands themselves are opposite the projecting ridges, and are extended upwards into the several leaf-teeth. Between the ridges are regions of green chlorophyll-parenchyma, while the whole is invested by a well-marked epidermis, with curiously elaborate stomata: these are ranged along the furrows, and so are opposite the photosynthetic tissue. The anatomy is clearly that of a semi-aquatic plant with its reduced vascular tissue and large air-spaces.

The sporangia of *Equisetum* are borne upon lateral appendages of the axis, sporangiophores, which are disposed in whorls, and are associated in definite strobili or cones, borne distally (fig. 7, A). Each sporangiophore consists of a stalk that expands into a peltate disc, from the inner surface of which some



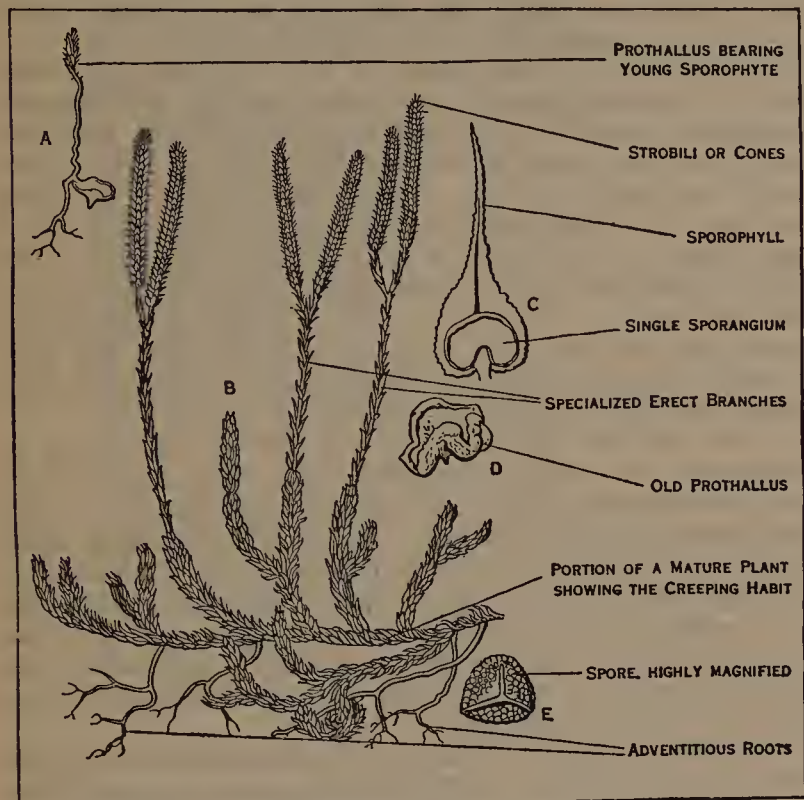
FROM (A, B, C) STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 7.—LARGER HORSETAIL (*EQUISETUM TELEMATEIA*)

six to nine large sporangia hang parallel with the stalk (fig. 7, B, C). A single vascular strand passing through the stalk supplies a branchlet to each sporangium. These arise as massive growths from the first, and each produces a large output of homosporous spores (eu-sporangiate). The spores themselves are large; in ripening the outermost layer of the wall of each splits along spiral lines, giving rise to four elaters that straighten out when dry, and close round the spore in damp air. They are effective in forcing open the sporangium, which dehisces by a longitudinal



slit: and those of different spores hooking together, the spores are grouped in germination, a matter of importance since the sexes are usually borne on separate prothalli. The spores germinate at once, producing each a green prothallus, which may be filamentous, flattened, or irregularly lobed. The smaller bear sunken antheridia, each with numerous spermatocytes, from which spermatozoids are liberated on access of water. The larger bear archegonia. The conditions of syngamy and formation of the embryo are essen-



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 8.—A CLUB-MOSS (*LYCOPodium CLAVATUM*)

tially as in ferns; but here the embryo has its apex directed to the archegonial neck (exoscopic), and it grows out directly into the apex of the young plant, successive whorls of leaves arising laterally upon it; a root derived from the basal region fixes the young plant in the soil. Notwithstanding the differences of detail, the life-cycle of a horsetail is comparable as a whole with that of a fern.

A greatly added interest in *Equisetum* arises from comparison with allied fossils; for not only were these numerous and of early occurrence, but they attained dendroid proportions, while some were heterosporous. They are grouped as the Calamariaceae, which will be specially treated elsewhere (see PALAEOBOTANY).

The Equisetales, thus comprising the Equisetaceae and the Calamariaceae, form a natural and closely related class, of which the nearest affinity was with the Sphenophyllales, but with some degree of relation also with the Psilotales; all of these being sporangiophoric Pteridophytes.

**V. Lycopodiales.**—This class comprises a considerable number of species now living widely distributed upon the earth, and known as *club-mosses*; though they are in fact vascular plants, and quite distinct from the true mosses. They are all relatively small, and indeed insignificant as features in the present flora, compared with the fossil types which, though they may have included a number of relatively small species, comprised also some of the largest plants of the forests of the coal period. It may be that among the lycopods no actual diminution in size took place as time went on, but rather that the types which were always small survived, while the giant members of the group became extinct.

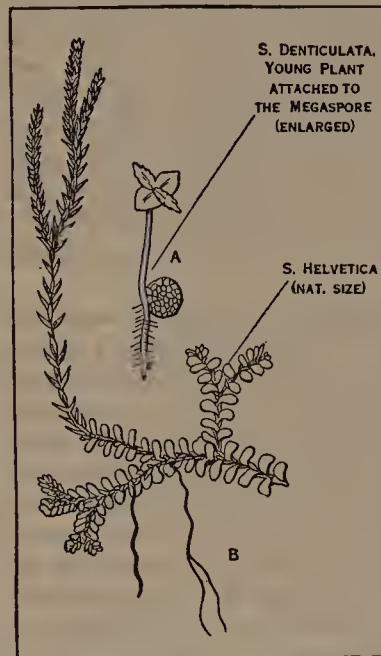
The features which all club mosses have in common are that the leaves are relatively small and simple in form (*microphyllous*), while the sporangia are seated singly, one in the axil of each leaf of the fertile region, or spreading outwards on its base. This marks off the Lycopodiales clearly from the sporangiophoric Pteridophytes on the one hand, and from the Filicales on the other. As in the former, however, the axis is dominant in the adult shoot, and forks equally or unequally. According to the

position assumed by the stem the habit of living club mosses is upright or pendent; but frequently, as in the stag's horn moss common on Scottish hills, with its creeping stem rooted in the soil, and bearing upright fruiting branches (fig. 8, B).

The class is divided systematically according to the presence or absence of a *ligule*, which is a small scale-like body borne on the upper surface of each leaf, near its base. Those in which no ligule is present, the *ELIGULATAE*, include *Lycopodium* and *Phylloglossum*, together with certain early fossils designated *Lycopodites*; those which possess a ligule, the *LIGULATAE*, include *Selaginella* and *Isoetes*, and with these are associated the fossil *Lepidodendraceae* and *Sigillariaceae*. The distinction is accentuated by the fact that the former are all homosporous, the latter heterosporous.

**A. Lycopodiales Eligulatae.** *Lycopodium* comprises about 100 species of small plants of varied habit, creeping, shrubby or epiphytic. The construction of the shoot is uniformly microphyllous, the bifurcating stem dominating the conformation of the whole plant. The leaves are simple and small, and in some species uniform throughout the plant. In others the sterile leaves are larger than the membranous sporophylls, the latter being associated in definite strobili, or cones (fig. 8, B). The former probably represent the more primitive type. Each of the isolated sporangia is seated at the base of its sporophyll; it is large, and kidney-shaped, with a short massive stalk, and it dehiscence like an oyster-shell, in a plane parallel to that of the leaf. The arrangement of the leaves is sometimes in regular whorls, but frequently it is according to some more or less interrupted spiral scheme. The plant is fixed at its base by roots which spring endogenously from the stem, and show bifurcation.

The stem of *Lycopodium* is seen in transverse section to be surrounded by a bulky and often indurated cortex, and traversed by a stele continued to the apical cone itself, while from each leaf a minute vascular strand passes to its periphery. In the young stem there is a solid woody core, surrounded by phloem and ill-defined sheaths. But in fully-grown stems the core may be invaded by tracts of phloem, moulding it into a cruciform or stellate transverse section, or even separating it into distinct radiating plates, or permeating it to form a sort of woody sponge.



FROM STRASBURGER, "LEHRBUCH DER BOTANIK" (GUSTAV FISCHER)

FIG. 9.—A CLUB-MOSS (*SELAGINELLA*)

canal-cells. But the egg is deeply seated, and produces an embryo with a suspensor. This thrusts the embryo deep into the prothallus, where it often develops juvenile characters of importance for comparison. The most striking of these is the swollen "protocorm," a tuberous growth seen in *Hornea*, and present also in *Phylloglossum*. Bursting out from the prothallus the embryo develops shoot and root, the former in the underground types finding its way upwards to the soil-level (fig. 8, A).

The sporangia are massive from the first, and vary slightly in spread along the leaf-surface, a point of interest for comparison with the ligulate types. Each produces after the usual tetrad-division a large number of homosporous spores, which germinate slowly. The prothalli produced from them, and the embryology that follows, vary more than is usual in a single genus. The prothallus sometimes grows at soil-level and is green (*L. cernuum*); but often it is underground and wholly saprophytic (*L. clavatum*, fig. 8, D, A). Whatever its form, the sex-organs are massive and deeply sunk, and both are present on the same prothallus. The antheridia produce numerous biciliate spermatozoids; the archegonia vary in length of neck, and sometimes have numerous



*B. Lycopodiales Ligulatae.* *Selaginella* comprises some 500 species, widely spread through the tropics, some native on temperate hill stations. The latter, chiefly of exposed habit, have radial symmetry, but most *Selaginellas* are dorsiventral, and live under shade. The genus shares the leading features of *Lycopodium*, but it differs in the presence of a ligule, and in the fact that all the species are heterosporous. Various *Selaginellas* are favourite greenhouse plants, and the fan-like spread of the delicate branches with their dimorphic leaves is well known (fig. 9, B); also the strange rhizophores springing from points of branching of the shoot, which turning downwards give rise to the true roots, being themselves organs of indeterminate morphological nature. It will be unnecessary to describe the vegetative organs or their anatomy in detail; the chief comparative interest lies in the propagative process.

The sporangia are borne on radially-constructed distal cones. A single sporangium similar to that of *Lycopodium*, is borne just above the insertion of each sporophyll, with the ligule protecting it from without. The microsporangia are brownish when ripe and the megasporangia pale in colour, and both may be borne on a single cone. They appear all alike up to the stage when the numerous spore-mother-cells are formed. If all the spore-mother-cells undergo tetrad-division numerous microspores resembling those of *Lycopodium* result. But in a megasporangium only one, or at most a few of them form tetrads, and the resulting spores are large with a rugged wall; the number matured in a single sporangium may vary from one to four, or some multiple of four. On germination each microspore produces a small number of spermatozoids from a very reduced prothallus; but the large megaspore forms a more bulky prothallus, which, projecting from the disrupted wall, bears archegonia. One of these on fertilization develops an embryo with a suspensor. The essentials of the process are as in *Lycopodium*, though the details are different. As the sporeling develops its leafy shoot grows upwards, and its root downwards; with the megaspore attached laterally the whole has the appearance of a seedling of some flowering plant (fig. 9, A). This is clearly an advance upon *Lycopodium*.

The other genus *Isoetes* is peculiar in habit and in habitat, yet shares many of the characteristics of *Selaginella*. It contains about 50 species of tufted herbs, mostly living at the bottom of fresh-water lakes, though a few are amphibious or terrestrial. The plant consists of a short massive lobed stock, bearing crowded awl-shaped leaves of considerable length. Each bears a ligule on its upper surface, and when fertile as any one of them may be, a large cake-like sporangium lies between this and the axis. Roots with dichotomous branching arise from furrows between its lobes. The sporangia are heterosporous, and propagation is essentially similar to that in *Selaginella*; but there is no suspensor, and the spermatozoids are multi-ciliate.

A chief interest in these Ligulate types lies in their comparison with the Lepidodendraceae and Sigillariaceae, for these are also ligulate and heterosporous (see PALAEOBOTANY). These fossils attained dendroid dimensions, and though the primary vascular system was not unlike that of the modern Lycopods, they often differed in having secondary growth with an active cambium. In *Isoetes* there is a sluggish secondary growth in the short stock, which itself shows certain analogies with the Stigmarian trunks of the gigantic fossils. Since any of the leaves of *Isoetes* may be fertile the whole plant appears as a strobilus of the same nature as *Lepidostrobus*, seated upon a Stigmarian base. In fact *Isoetes* is like a telescoped, but still living, fossil.

**VI. Filicales.**—The Filicales may be held as comprising all the living Megaphyllous Pteridophytes, together with such fossils as show essentially similar characters. But the mere fact that their leaves are relatively large in proportion to the stem that bears them is not a sufficient diagnosis. Some Lycopods (*Isoetes*, *Sigillaria*) share this character, and megaphylly is possible in any of Pteridophytes. But as a matter of fact, excepting *Isoetes*, none such are now living other than the Filicales. The most distinctive feature of ferns, however, is that *on the relatively large leaves many sporangia are borne, either singly or in groups (sori)*.

Ferns are represented at the present day by about 150 genera,

and 6,000 species. Some are minute, others attain considerable size as tree ferns; but none can be reckoned among the largest of living plants, nor is there fossil evidence that ferns ever attained extreme dimensions. Their geographical spread is general; some few are arctic, but ferns increase in numbers both of species and of individuals towards the Equator. Most are mesothermal hygrophytes, *i.e.*, they flourish under moist conditions with a moderate temperature; and the majority are shade-loving. Hence their headquarters are in the mountains of the tropics, where they form a considerable part of the undergrowth below the forest canopy. But their habitat is variable; some specialized types are actually aquatic, while others are able to withstand conditions of moderate, some even of extreme drought. Ferns are much richer in genera, species and individuals than any other living Pteridophytes. They present the climax of successful development in homosporous vascular plants. They show also a high degree of variety both in their vegetative and their propagative characters; these provide good diagnostic features for their classification. They have a full and long palaeontological history that stretches back to Palaeozoic times. The geological record can therefore be used as a valid check upon the conclusions drawn from the comparison of living types.

It has been said that the Palaeozoic period was the age of ferns, and it is true that "fern-like" leaves were then common. But it has now been shown that many of these belonged to seed-plants ranked as Pteridosperms, a class long since extinct, which also had fern-like leaves (see PALAEOBOTANY). It is not improbable that they represent a stock more distinct from ferns than the similarity of their foliage would suggest, for they had advanced early to seed-formation. It may be left as an open question whether or not both may have had far back in their evolution some common origin.

The life-history already described at the opening of this article holds for ferns generally, so that the grouping and natural classification of the class must depend upon differences of detail other than the life-history itself. A general comparison of them led long ago to the recognition of eight main families, which may here be placed in the reverse order to that first given by Mettenius (1856):—

- |                     |                       |
|---------------------|-----------------------|
| I. Ophioglossaceae. | V. Gleicheniaceae.    |
| II. Marattiaceae.   | VI. Hymenophyllaceae. |
| III. Osmundaceae.   | VII. Cyatheaceae.     |
| IV. Schizaeaceae.   | VIII. Polypodiaceae.  |

This grouping in linear sequence places the more robust types first, and the more delicate last, while the rest take middle positions. The former have been styled by Von Goebel the *Eusporangiate ferns*, in which the sporangium is from the first a massive body, in the formation of which many cells co-operate; in the latter each sporangium arises from a single cell, and those ferns in which this is so were styled *Leptosporangiate*. Intermediate states exist, and these suggest that the whole series constitutes an evolutionary progression. If this be true the question arises which is the more primitive, and which the more advanced state? The importance of this question is enhanced by the fact that the sporangium is a mere index of a general difference of organization of the two contrasted types. In point of fact *the Eusporangiate ferns are relatively robust in their general constitution, while the Leptosporangiate are relatively delicate*. Thus the question is whether there has been in the course of evolution a progression from a robust to a delicate state, or the reverse. Since the Eusporangiate ferns find their correlatives in the fossils of Palaeozoic time and are relatively few to-day, while the specialized Leptosporangiate ferns are absent from the Palaeozoic rocks and comprise the bulk of living ferns, it is concluded that the general progression has been from a more robust ancestry towards a more delicate and precise constitution.

Having perceived this general scheme of progressive refinement, it cannot be assumed that the 150 genera, and 6,000 species have formed a simple sequence. In testing the question of their relationships it will become necessary to revise the methods in use by systematists, whose aims were primarily classification. They worked as a rule upon few criteria of comparison, drawn almost



exclusively from the sporophyte generation. A more exact comparison will be necessary not only as regards external form, but also of internal structure and development, both of the vegetative and the propagative organs, and it must be extended to both generations. The larger the number of the criteria used in comparison the more trustworthy will be the conclusions drawn from them. The criteria currently used in the comparison of ferns are these:

1. The external morphology of the shoot.
2. The initial constitution of the plant-body as indicated by segmentation.
3. The architecture and venation of the leaf.
4. The vascular system of the shoot.
5. The dermal appendages.
6. The position and structure of the sorus.
7. The indusial protections.
8. The characters of the sporangium, and the form and markings of the spores.
9. The spore-output.
10. The morphology of the prothallus.
11. The position and structure of the sexual organs.
12. The embryology of the sporophyte.

By the combined use of these criteria it has been possible to revise the natural groupings of ferns, sometimes amending but more often upholding the decisions of the earlier systematists. The main conclusions may be stated as follows: The *Eusporangiatae* include the living Ophioglossaceae, Marattiaceae and Osmundaceae, together with the fossil Coenopteridaceae (see PALAEOBOTANY). All these are Palaeozoic types, though they overlapped into the Mesozoic, and some representatives have even survived to the present day. With them are to be associated also the Schizaeaceae, Gleicheniaceae and Matoniaceae, all of which figured prominently in the Mesozoic, and are well represented among living ferns. In addition to many archaic features of the vegetative system they all possess relatively massive sporangia, which originate simultaneously, being produced either singly or in small numbers in the sori. They are collectively styled *Simplices*. Each sporangium has a relatively large spore-output.

The Ophioglossaceae and Marattiaceae appear to have ended blindly and left no further derivatives. But derivative phyla may be traced by comparison from each of the Schizaeaceae, Osmundaceae, and Gleicheniaceae, while to the Matoniaceae so closely allied, to the Dipterids, another phylum may be ascribed. The Schizaeaceae with their solitary marginal sporangia lead to the marginal Dicksoniaceae. The Osmundaceae have many features in common with *Plagiogyria*, while the superficial Gleicheniaceae link on to the Cyatheaceae, these being distinguished by their superficial sori from the marginal Dicksoniaceae. In both of these last-named families the sorus has become "*gradate*," i.e., after the distal sporangia have been formed on the receptacle, a sequence of further sporangia follows in *basipetal sequence*, the effect of which is that the drain of nutrition is spread over a longer period of time. This may well have been a real factor in the success of these families.

A third state of the sorus, which has a like effect to the last, and may either be initiated independently or by transition from the gradate, is the "*mixed*" state, where sporangia of different ages are irregularly *interpolated between those already present*. This is the final condition seen in the evolution of the Leptosporangiate ferns, and is found in all the more advanced types.

From such intermediate stocks as those mentioned some *six derivative phyla of advanced Leptosporangiate ferns* may be distinguished, each centring round some well-known genus. Two of these comparison shows to have been derived from the Dicksoniaceae, viz., the Davallioid ferns centred round *Davallia*, and the Pteroids round *Pteris*. The Gymnogrammoid ferns are naturally grouped round *Gymnogramme*, and may probably be traced from the Osmundaceae, with *Plagiogyria* as a suggestive link. The Cyatheaceae probably gave rise on the other hand to the Blechnoid ferns, with *Blechnum* as a central type; and the Dryopteroids round *Dryopteris*. Lastly, a quite considerable number of

genera may be traced as Dipteroid derivatives, from an ancestry suggested by *Matonia* and *Dipteris*. Thus at least six main evolutionary sequences of advanced Leptosporangiate ferns, with more or less pronouncedly "mixed" condition of their sori, may be referred in origin to types already distinct in Palaeozoic, or certainly in Mesozoic time. Each of these will have pursued its own phyletic advance independently of the others. Comparison reveals that most of them, or in some respects all, show parallel features of advance in form, vascular structure, soral characters, and sporangia, and particularly in the reduced spore-output from each sporangium. There is thus wide evidence of independent *homoplastic, and even convergent evolution* in the several phyla. In no respect is this clearer than in the distinctive feature of heterospory: for the Marsileaceae are referable in origin to a Schizaeoid source, while the Salviniaceae, whatever their actual relation, were of distinct origin from the Marsileaceae.

This brief abstract of the present position of the phyletic study of the Filicales can do no more than suggest how the matter stands to-day. Of all the Pteridophyta the ferns yield the most consecutive results. The living representatives of all the rest appear as isolated survivals, illuminated by fossil evidence, often as fragmentary and isolated as theirs. They raise as many evolutionary questions as they solve. It is only in the Filicales that it is possible, by placing together the evidence from palaeontology and that derived from the living flora, to reconstruct a story which, however incomplete, is sufficiently consecutive to serve as a basis for evolutionary opinion. The sum of it is for the ferns, as also for other Pteridophyta, that they have held their own to the present day as a class which has made the best of their amphibious existence by help of profuse production of homosporous spores. But from the point of view of descent, they have led on directly to no further type of land vegetation. The sources of this must be sought elsewhere.

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**INTEGUMENT**, the cell membrane enveloping the protoplasts of plants. It is composed of cellulose together with a number of other substances known as pectic compounds. In biology the term also implies the skin or external covering of an animal.

**NUTATION**. The name used in reference to the phenomena of certain organs in plants which bend alternately in opposite directions. In some cases the apex of the stem will describe a spiral movement, inclining to all points of the compass in succession; this being termed *circumnutation*. See PLANTS.

**PIN-EYED**, a botanical term for flowers which occur in two forms, one of which shows the stigma at the mouth of the corolla, as in the primrose. The term is contrasted with thrum-eyed, where instead of a single stigma a ring of five stamens is visible.

**IDIOBLAST**, a botanical term for an individual cell which is distinguished by its shape, size or contents, such as the stone-cells in the soft tissue of a pear.

**LILIACEAE**, in botany, a family of Monocotyledons belonging to the series Liliiflorae, and generally regarded as representing the typical order of Monocotyledons. The plants are generally perennial herbs growing from a bulb or rhizome, sometimes shrubby as in butcher's broom (*Ruscus*) or tree-like as in species of *Dracaena*, *Yucca* or *Aloe*. The flowers are with few exceptions hermaphrodite, and regular with parts in threes, the perianth which is generally petaloid occupying the two outer whorls followed by two whorls of stamens, with a superior ovary of three carpels in the centre of the flower; the ovary is generally three-chambered



with a number of anatropous ovules or axile placentas. The fruit is a capsule splitting along the septa (septicidal), or between them (loculicidal), or a berry; the seeds contain a small embryo in a copious fleshy or cartilaginous endosperm. Liliaceae is one of the larger families of flowering plants containing about 2,700 species in 250 genera being approximately one-eighth of the Monocotyledons; it is of world-wide distribution. It contains many useful plants (onion, leek, garlic) and garden plants (lily, tulip, hyacinth). The plants show great diversity in vegetative structure, which together with the character and mode of dehiscence of the fruit affords a basis for the subdivision of the family into tribes, eleven of which are recognized. The following are the most important tribes.

**Melanthioideae.**—The plants have a rhizome or corm, and the fruit is a capsule. Many are north temperate and three are represented in Britain, viz. *Tofieldia*, an arctic and alpine genus of small herbs with a slender scape springing from a tuft of narrow ensiform leaves and bearing a raceme of small green flowers; *Narthecium* (bog-asphodel), herbs with a habit similar to *Tofieldia*, but with larger golden-yellow flowers; and *Colchicum*, a genus with about 30 species including the meadow saffron or autumn crocus (*C. autumnale*). *Colchicum* illustrates the corm-development which is rare in Liliaceae, though common in the allied family Iridaceae. *Gloriosa*, well known in cultivation, climbs by means of its tendril-like leaf-tips; it has handsome flowers with recurved orange-red or yellow petals; it is a native of tropical Asia and Africa. *Veratrum* is an alpine genus of the north temperate zone.

**Asphodeloideae.**—The plants generally have a rhizome bearing radical leaves, as in asphodel, rarely a stem with a tuft of leaves as in *Aloe*, very rarely a tuber (*Eriospermum*) or bulb (*Bowiea*). The flowers are borne in a terminal raceme, the anthers open introrsely and the fruit is a capsule, very rarely, as in *Dianella*, a berry. *Asphodelus* (asphodel) is a Mediterranean genus; *Simethis*, a slender herb with grassy radical leaves, is a native of west and southern Europe extending into south Ireland. *Anthericum* and *Chlorophytum*, herbs with radical often grass-like leaves and scapes bearing a more or less branched inflorescence of small generally white flowers, are widely spread in the tropics. Other genera are *Funkia*, native of China and Japan, cultivated in the open air in Britain; *Hemerocallis*, a small genus of central Europe and temperate Asia—*H. flava* is known in gardens as the day lily; *Phormium*, a New Zealand genus to which belongs New Zealand flax, *P. tenax*, a useful fibre-plant; *Kniphofia* (red-hot poker), South and East Africa, several species of which are cultivated; and *Aloe*. A small group of Australian genera closely approach the family Juncaceae in having small crowded flowers with a scarious or membranous perianth; they include *Xanthorrhoea* (grass-tree or black-boy) and *Kingia*.

**Allioideae.**—The plants grow from a bulb or short rhizome; the inflorescence is an apparent umbel formed of several shortened monochasial cymes and subtended by a pair of large bracts. The largest genus *Allium* has about 325 species—7 are British; *Agapanthus* or African lily is a well-known garden plant; in *Gagea*, a genus of small bulbous herbs found in most parts of Europe, the inflorescence is reduced to a few flowers or a single flower; *G. lutea* is a local and rare British plant.

**Lilioideae.**—Bulbous plants with a terminal racemose inflorescence; the anthers open introrsely and the capsule is loculicidal. It contains about 30 genera, several being represented in Britain. The typical genus *Lilium* and *Fritillaria* are widely distributed in the temperate regions of the northern hemisphere; *F. meleagris*,

snake's head, is found in moist meadows in some of the southern and central English counties; *Tulipa* contains about 50 species in Europe and temperate Asia, and is specially abundant in the dry districts of central Asia; *Lloydia*, a small, slender alpine plant, widely distributed in the northern hemisphere, occurs on Snowdon in Wales; *Scilla* (squill) is a large genus, chiefly in Europe and Asia—*S. nutans* is the blue-bell or wild hyacinth; *Ornithogalum* (Europe, Africa and west Asia) is closely allied to *Scilla*—*O. umbellatum*, star of Bethlehem, is naturalized in Britain; *Hyacinthus* and *Muscari* are chiefly Mediterranean; *M. racemosum*, grape hyacinth, occurs in sandy pastures in the eastern counties of England. To this group belong a number of tropical and especially South African genera, such as *Albuca*, *Urginea*, *Drimis*, *Lachenalia* and others.

**Dracaenoideae.**—The plants generally have an erect stem with a crown of leaves which are often leathery; the anthers open introrsely and the fruit is a berry or capsule. It contains a small number of genera, several of which, such as *Yucca*, *Dracaena* and *Cordyline* include arborescent species in which the stem increases in thickness continually by a centrifugal formation of new tissue; an extreme case is afforded by *Dracaena Draco*, the dragon-tree of Teneriffe. *Yucca* and several allied genera are natives of the dry country of the southern and western United States and of Central America. *Dracaena* and the allied genus *Cordyline* occur in the warmer regions of the Old World.

**Asparagoideae.**—Plants growing from a rhizome; fruit a berry. *Asparagus* contains about 120 species in the dryer, warmer parts of the Old World; it has a short creeping rhizome, from which springs a slender, herbaceous or woody, often very much branched, erect or climbing stem, the ultimate branches of which are flattened or needle-like, leaf-like structures (*cladodes*), the true leaves being reduced to scales or, in the climbers, forming short, hard, more or less recurved spines. *Ruscus aculeatus* is butcher's broom, an evergreen shrub with flattened leaf-like cladodes, native of the southerly portion of England and Wales; the small flowers are unisexual and borne on the face of the cladode; the male contains three stamens, the filaments of which are united to form a short stout column on which are seated the diverging cells of the anthers; in the female the ovary is enveloped by a fleshy staminal tube on which are borne three barren anthers. *Polygonatum* and *Maianthemum* are allied genera with a herbaceous leafy stem and, in the former axillary flowers, in the latter flowers in a terminal raceme; both occur rarely in woods in Britain; *P. multiflorum* is the well-known Solomon's seal of gardens, so called from the seal-like scars on the rhizome of stems of previous seasons, the hanging flowers of which contain no honey, but are visited by bees for the pollen. *Convallaria* is lily of the valley; *Aspidistra*, native of the Himalayas, China and Japan, is a well-known pot plant; its flowers depart from the normal arrangement of the family in having the parts in fours (tetramerous). *Paris*, including the British Herb Paris (*P. quadrifolia*), has solitary tetra- to poly-merous flowers terminating the short annual shoot which bears a whorl of four or more leaves below the flower; in this and in some species of the nearly allied genus *Trillium* (chiefly temperate North America) the flowers have a fetid smell, which together with the dark purple of the ovary and stigmas and frequently also of the stamens and petals, attracts carrion-loving flies, which alight on the stigma and then climb the anthers and become dusted with pollen; the pollen is then carried to the stigmas of another flower.

**Luzuriagoideae** are shrubs or undershrubs with erect or climbing branches and fruit a berry. *Lapageria*, a native of Chile, is a favourite greenhouse climber with fine bell-shaped flowers.

**Smilacoideae** are climbing shrubs with broad net-veined leaves and small dioecious flowers in umbels springing from the leaf-axils; the fruit is a berry. They climb by means of tendrils, which are stipular structures arising from the leaf-sheath. *Smilax* is a characteristic tropical genus containing about 210 species; the dried roots of some species are the drug sarsaparilla.

The two tribes *Ophiopogonoideae* and *Aletroideae* are sometimes removed from the Liliaceae and placed in the family, Haemodoraceae. The plants have a short rhizome and narrow or lanceo-



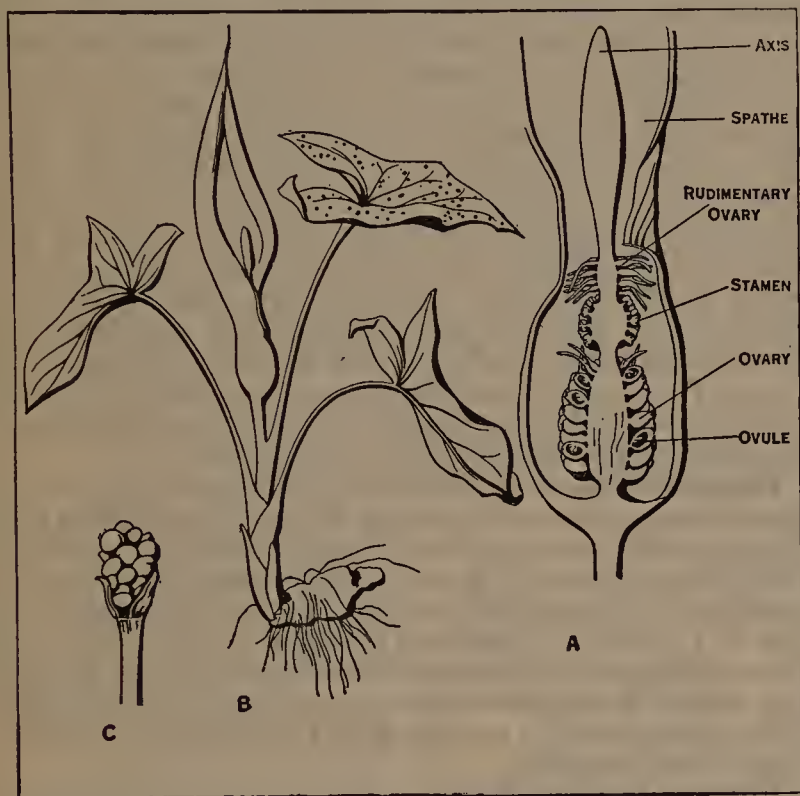
FROM H. J. ELWES, "MONOGRAPH OF THE GENUS LILIUM"  
LONG-FLOWERED WHITE LILY (*LILIUM LONGIFLORUM*). A, SCALY BULB, WITH TWO SMALL BULBS



late basal leaves; and they are characterized by the ovary being often half-inferior. They contain a few genera chiefly old world tropical and subtropical. Leaves of species of *Sansevieria* yield a valuable fibre, and tubers of *Ophiopogon japonicus* are edible.

**ARACEAE** or **AROIDEAE**, the arum family, a large group of monocotyledonous plants containing upwards of 100 genera and more than 1,000 species, of which the cuckoo-pint in Great Britain, and the jack-in-the-pulpit, found in eastern North America, are familiar examples. Neither of these small plants, however, gives more than meagre indication of the characters of this interesting plant family which attains its most conspicuous development in the Tropics. The aroids are generally herbaceous, often, however, reaching gigantic size; but they are sometimes shrubby climbing plants. Many are peculiar in form and habit and grotesque in appearance. Various climbing species of *Philodendron* have feeding roots which penetrate the soil and clasping roots that fix the plant to its support. Some are epiphytes, a few, as the water lettuce, are floating plants.

The leaves, which show great variety in size and form, are generally broad and net-veined, though sometimes sword-shaped and parallel-veined. In *Arum* (*q.v.*) the blade is simple. In other



A. FROM GROOM, "ELEMENTARY BOTANY"; B. FROM STRASBURGER, "TEXTBOOK OF BOTANY"  
WILD ARUM (*ARUM MACULATUM*), COMMONLY "LORDS AND LADIES"  
A. Details showing mode of development of the flowers  
B. The plant itself  
C. The berries, exposed when the large sheathing leaf that encloses them withers

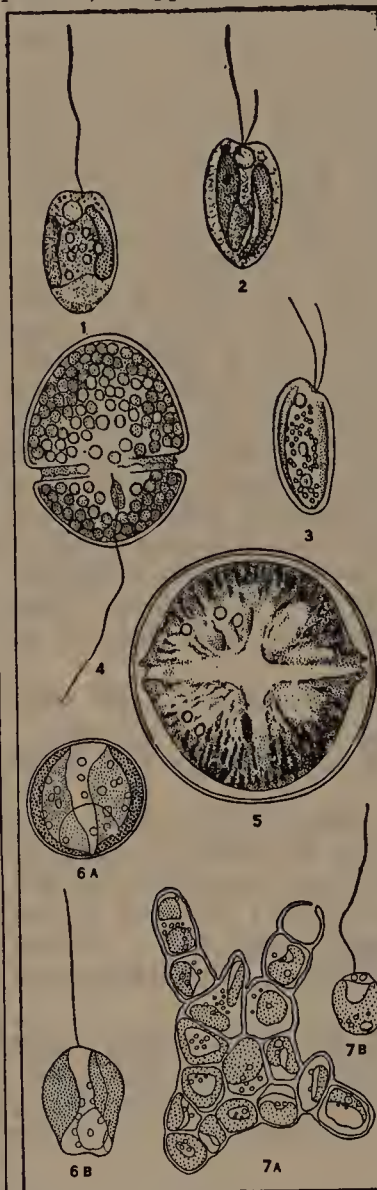
genera the leaves are divided and sometimes very large; those of *Dracontium* (tropical America) may be 15 ft. high. In the ceriman (*Monstera*) the large perforated leaves appear as if cut full of holes. The small flowers are crowded on thick, fleshy spikes, which are usually enveloped by a large leaf (bract), the spathe, which is often the most conspicuous feature of the plant. For example, in the cuckoo-pint the spathe is large and green; in the jack-in-the-pulpit it is purple-striped; in the callas it is white or yellow; and in the anthuriums it is scarlet. In *Amorphophallus*, an East Indian genus, the "flower" (spathe and spadix) often exceeds 3 ft. in length. The true flowers are often extremely simple, sometimes, as in *Arum*, reduced to a single stamen or pistil. The fruit is a berry. Usually the plants contain a poisonous acrid juice. The underground stems (rhizomes or tubers) are rich in starch; those of the tropical taro (*q.v.*) providing a valuable article of food. From the rhizomes of the cuckoo-pint Portland arrowroot was formerly prepared. The starchy corms of the jack-in-the-pulpit were utilized for food by the Indians of eastern North America.

Besides the cuckoo-pint, the *Acorus Calamus* (*q.v.*) or sweet flag occurs in Great Britain, though it is supposed to have been

introduced. In North America about 15 native species of aroids are found, chiefly in the southern and eastern United States. Among these are the jack-in-the-pulpit, green dragon, golden-club, sweet flag, wild calla, water-lettuce (*qq.v.*) and skunk-cabbage. Only one native species, the western skunk-cabbage (*Lysichiton kamschatensis*), occurs on the Pacific coast. Because of their unusual foliage and inflorescence numerous species of *Alocasia*, *Anthurium*, *Caladium*, *Calocasia*, *Dieffenbachia*, *Scindapsus*, *Xanthosoma*, and other genera are grown in greenhouses for ornament and as curiosities. A good series of tropical aroids may be seen in the aroid house at Kew.

**ULMACEAE**, a family of dicotyledonous trees, the best known and most important members of which are the elms (*q.v.*), forming the genus *Ulmus*. The family contains 13 genera and about 130 species. *Celtis australis* is the nettle-tree, the fruit of which is edible. *C. occidentalis* is the hackberry (*q.v.*).

**PROTOPHYTA.** The designation Protophyta ("first plants") is applied to all simple one- and several-celled organisms



FROM "SÜSSWASSERFLORA," AND HARTMAN & PASCHER, "ARCHIVES FÜR PROTISTENKUNDE" (GUSTAV FISCHER)

#### TYPES OF PROTOPHYTA

1. Chromulina, motile cell (Chrysophyceae).
2. Ochromonas, motile cell.
3. Cryptomonas, motile cell.
4. Glenodinium, motile cell (Dinophyceae).
5. Hypnodinium, motionless cell (same).
- 6a. Chrysosphaera, motionless cell (Chrysophyceae).
- 6b. Chrysosphaera, Zoospore (same).
- 7a. Thallochrysis, branched filament (same).
- 7b. Thallochrysis, Zoospore (same)

that obtain their nourishment after the manner of a plant. Such forms probably afford a fairly accurate picture of what the early stages in the evolution of the vegetable kingdom were like. The simpler Algae (*q.v.*) are of course embraced in the Protophyta. Together with Protozoa (*q.v.*) the latter constitute the Protista, which comprise all the most elementary forms of life. There are many classes of Protista, some definitely holophytic (*i.e.*, feeding like a plant), others definitely holozoic (*i.e.*, taking in solid food like an animal), whilst still others exhibit a mingling of plant and animal characteristics, so that it depends to some extent on personal bias whether they be referred to Protozoa or Protophyta. A rigid definition is impossible and undesirable. The Protophyta may, however, justifiably be taken to include all simple organisms carrying on photosynthesis. In this process organic compounds are built up from carbon dioxide and water with the help of solar energy absorbed by pigments which are held within the cells in special protoplasmic bodies, the *chromatophores*. The latter always contain green chlorophyll which predominates in the green Algae (Isokontae), but in many classes is associated with other pigments (yellow, brown, red, etc.) which give a distinctive coloration to their respective members. Moreover, the carbon-compounds, that accumulate in the cells after active photosynthesis, vary in the different classes (starch, fat, leucosin, etc.), an indication that distinct metabolic processes are associated with the diverse types of pigmentation. The various classes can thus be distinguished on a physiological basis by their special mechanisms for nutrition.

**Motile and Stationary Forms.**—Many of the simplest unicellular Protophyta are actively motile with the help of delicate



protoplasmic threads, the cilia or flagella, whose number and arrangement is usually distinctive for each class (figs. 1-4). Every class, however, also includes motionless organisms of varied type, partly unicellular (figs. 5, 6a) and partly multicellular (fig. 7a). Many of these reproduce themselves by means of naked swimmers (zoospores), which are essentially similar to the motile unicellular individuals of their class and which, after a period of movement, lose their cilia and give rise to the stationary organism. This fact has led to the assumption—now generally accepted—that such sedentary forms have evolved from motile unicells in much the same way as they arise from their zoospores during their individual life-history. It is, however, probable that in some series of Protophyta (e.g., Myxophyceae) no motile organisms were ever evolved, even the unicellular individuals being motionless from the first.

In certain classes of Protophyta (Isokontae, Heterokontae, Myxophyceae) the majority of the known genera are stationary, i.e., they exhibit the essentially plant-like characteristic of immobility. These are usually grouped under the name of Algae (q.v.) which also comprise some series that have evolved beyond the level of the Protophyta and in which no simple forms are known (cf. below). In other classes of Protophyta, however, the majority of the species are motile and, for this reason, and also because the simpler individuals are ordinarily not clothed by a cell-wall, they have been regarded as something apart from the Algae more nearly related to Protozoa and grouped as Flagellata. But in several of these classes (Peridinieae, Chrysomonadineae) motionless unicellular and filamentous types corresponding to those found in Isokontae, Heterokontae, etc. (see ALGAE) have been discovered in recent times, and there is thus no valid reason for separating them from those Protophyta that are grouped as Algae.

A number of colourless Protista resemble plants, since they feed mainly by absorbing (organic) solutions and not by ingesting solid particles, i.e., they are saprophytes or parasites. Such forms are probably in part descended from holophytic types which have lost their chromatophores, while others may have been devoid of them from the first. From such primitively colourless Protophyta various series of fungi may have originated, although some fungi may have been derived from pigmented types by loss of chromatophores.

**Classification.**—The following is an epitome of the chief classes of pigmented Protophyta:—

1. ISOKONTAE (Chlorophyceae or green Algae), pure green forms, see ALGAE.

2. HETEROKONTAE (Yellow-green Algae), see ALGAE.

3. CHRYSOPHYCEAE, with few brown or orange-coloured chromatophores without pyrenoids (see ALGAE), producing fat and leucosin; motile forms (Chrysomonadineae) with one or two cilia at the front end; resting stages (cysts) with a silicified membrane composed of two unequal pieces; sometimes holozoic (figs. 1, 2, 6 and 7).

4. CRYPTOPHYCEAE, usually with two large, mostly brown chromatophores, with pyrenoids, producing starch or other similar carbohydrates; motile forms (Cryptomonadineae) asymmetrical, commonly flattened, with a sloping front end bearing two slightly unequal cilia (fig. 3).

5. DINOPHYCEAE (Peridinieae), with usually many, yellow or brown, discoid chromatophores, producing starch and oil; motile cells (Dinoflagellata) with a transverse furrow harbouring a transverse cilium and a less defined longitudinal furrow with a backwardly directed cilium (fig. 4). The advanced forms have an elaborate envelope.

6. EUGLENINEAE, with pure green chromatophores, sometimes with pyrenoids, producing paramylon; motile stages with one, or rarely two, flagella arising from a canal-like invagination at the front end. Very few sedentary types known.

7. MYXOPHYCEAE (Cyanophyceae or blue-green Algae), see ALGAE.

Several classes of Algae are omitted, because they include only relatively specialized forms, viz., the Diatoms (Bacillariales, q.v.), and the brown and red seaweeds (Phaeophyceae and Rhodophyceae, see ALGAE). They are, however, likewise distinguished

by their pigmentation, the products of photosynthesis, and the characteristics of the motile stages (when present), as well as by other peculiarities. No doubt each originated from simple forms parallel with those found in the classes of Protophyta, but which have become extinct or are not yet known. Should such simple forms ever be discovered they would naturally be included in the Protophyta.

**Range of Form.**—Most classes exhibit a more or less extensive range from simple unicells to branched multicellular filaments. Examples of these varied types, as far as they occur in Isokontae, Heterokontae, and Myxophyceae, are given in the article ALGAE and there, too, will be found a consideration of their relation to one another and of the ordinary course of reproduction. One can distinguish motile and motionless unicells colonies of motile and motionless individuals, palmelloid forms with numerous cells embedded in mucilage, simple and branched filaments, etc. Analogous forms, often almost identical in shape though with the differences in pigmentation, etc., characteristic of the relevant groups are met with in most classes of holophytic Flagellata. Thus, *Chrysosphaera* (fig. 6) is a spherical unicell, similar to *Chlorococcum* (Isokontae) or *Halosphaera* (Heterokontae), but it possesses the orange chromatophores and leucosin of Chrysophyceae and reproduces by zoospores closely resembling a *Chromulina*, one of the motile unicells of that class; similarly *Hypnodinium* (fig. 5) is such a motionless member of Dinophyceae, whose protoplasmic body before dividing during reproduction acquires temporarily the typical transverse and longitudinal furrows. Palmelloid forms, analogous to *Tetraspora* (Isokontae), are seen in *Phaeosphaera* (Chrysophyceae) and *Phaeococcus* (Cryptophyceae), while filamentous types are represented by *Phaeothamnion* or *Thallochrysis* (fig. 7) (Chrysophyceae) and *Dinothrix* (Dinophyceae), all reproducing by zoospores resembling closely the motile unicells of their particular classes. Further details cannot be given in the confines of a short article, but it will be clear that there is a far-going parallelism in the evolution of the different classes of Protophyta.

**Reproduction.**—The reproductive processes are of the simplest kind, most commonly consisting in a mere division of the individual into two parts, which in the motile forms may even take place during movement. Reproduction by zoospores, as already mentioned, is frequent in the more advanced stationary forms (figs. 6, 7). Sexuality, altogether lacking in the Myxophyceae, is rare and restricted to the higher forms in most classes. Oogamy (see ALGAE) is encountered alone in the Isokontae, where altogether the reproductive methods show a greater elaboration than among other Protophyta.

**Relation to Other Groups.**—The definite range from simple to complex implies an upgrade evolution which is recognizable also in the reproductive processes. As far as present knowledge goes, however, the multicellular filamentous types are of the simplest kind in most Protophyta. Even when branching occurs, there is no differentiation among the cells and the formation of reproductive units takes place in the simplest possible way. In other words these classes have ended blindly without developing far in the direction of the multicellular plant and it is only in Isokontae (as well as in Phaeophyceae and Rhodophyceae which, as explained above, must have had a Protophyte ancestry) that a considerably greater specialization is found; and this is accompanied by more complex reproductive methods and the development of an oogamous sexual process. While in the two classes of seaweeds massive and complex bodies have been evolved, this is not the case in the green Algae, although in other respects their advanced forms are almost as highly specialized as those of seaweeds. The absence of more elaborate types in Isokontae is probably due to their further evolution into land-plants in the far past, just as the simpler (extinct) Phaeophyceae and Rhodophyceae evolved into the seaweeds of the present day. In the same way other classes of Protophyta must have given rise to the various groups of fungi. There is little evidence of relationship between the known classes of Protophyta; most, if not all, seem to represent separate attempts at the evolution of a holophytic organism. The occasional resemblances to classes of



Protozoa are no doubt due to the fact that plant and animal tendencies were not clearly segregated in all the different evolutionary series.

**BIBLIOGRAPHY.**—For a general account of Protophyta, see G. S. West and F. E. Fritsch, *British Freshwater Algae* (Cambridge, 1927); A. Pascher, *Süßwasserflora Deutschlands, Österreichs und der Schweiz* (Jena, 1914 and onwards, esp. Heft 1, 2 and 4); and F. E. Fritsch, *Pres. Address to Section K, British Ass'n.* (1927). (F. E. F.)

**ALISMACEAE**, in botany, a family of monocotyledons belonging to the series Helobiae, and represented in Britain by the water plantain, *Alisma Plantago*, the arrow-head, *Sagittaria*, the star-fruit, *Damasonium*, and flowering rush, *Butomus*. They are marsh or water-plants with generally a stout stem (*rhizome*) creeping in the mud, radical leaves and a large, much branched inflorescence. The submerged leaves are long and grass-like, the floating leaves oblong or rounded, while the aerial leaves are borne on long, thin stalks above the water, and are often arrow-shaped at the base. The flower-bearing stem is tall; the flowers are borne in whorls on the axis as in arrow-head, on whorled branchlets as in water plantain or in an umbel as in *Butomus* (see fig.). They are regular and rather showy, generally with three greenish sepals, followed in regular succession by three white or purplish petals, six to indefinite stamens and six to indefinite free carpels. The fruit is a head of achenes or follicles. The flowers contain honey, and attract flies or other small insects by which pollination is effected. There are about 75 species in eleven genera, widely distributed in temperate and warm zones. *Alisma Plantago* (see fig.), a common plant in Britain (except in the north) in ditches and edges of streams, is widely distributed in the north temperate zone and on mountains.

In the United States and Canada the family is represented by about 40 native species, some three-fourths of which are arrow-heads. Among the other representatives are the cosmopolitan water plantain, two species of bur-head (*Echinodorus*), the dwarf bur-head (*Helianthium parvulum*) and the fringed water plantain or star-fruit (*Damasonium californicum*) of California. (See ARROW-HEAD.)

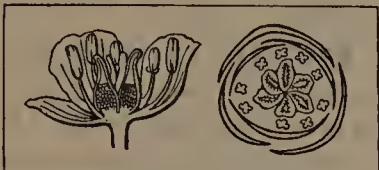
### AMARYLLIDACEAE,

the amaryllis family, a numerous group of monocotyledonous plants, closely allied to the lily family (Liliaceae). Familiar representatives are the daffodil, jonquil, snowdrop, snowflake and tuberose (*qq.v.*). The family comprises about 90 genera and 1,050 species, found chiefly in tropical and subtropical regions. Many are bulbous plants of arid lands, leafing only in spring or after rains. A large number bear handsome lily-like flowers, often popularly called lilies, as Amazon lily (*Eucharis grandiflora*), spider lily (*Hymenocallis* sp., *Pancratium* sp.) and zephyr lily (*Zephyranthes* sp.). Among the larger genera are *Agave*, *Crinum*, *Hippeastrum*, *Hypoxis* and *Narcissus*. Various species of *Agave* yield valuable fibres, as henequen, pita and sisal hemp; the bulbs of some species are used in medicine, while those of the South African belladonna lily (*Amaryllis Belladonna*) and the buphane (*Buphane disticha*) are highly toxic, the latter furnishing a Kafir arrow-poison. Representatives of more than 40 genera are grown as ornamental

plants in greenhouses and gardens. Native plants of the family in the British Isles are the yellow daffodil (*Narcissus Pseudo-Narcissus*), the snowdrop (*Galanthus nivalis*) and the summer snowflake (*Leucojum aestivale*). In North America there are more than 40 native species; these are found chiefly in the southern and the south-western United States and belong mostly to the genera *Agave*, *Hymenocallis* and *Zephyranthes*. Of those native to the eastern United States, the best known are the atamasco lily (*Zephyranthes Atamasco*), cultivated for its handsome flowers, and the yellow star-grass (*Hypoxis hirsuta*), the only representative extending northward into Canada. (See AGAVE; AMARYLLIS; HEMP; HIPPEASTRUM; LILIACEAE; NARCISSUS; SISAL HEMP.)

**ANONACEAE**, the custard-apple family, an important group of dicotyledonous plants allied to the magnolias (*q.v.*). They are chiefly tropical shrubs and trees and comprise about 80 genera and 820 species. The leaves are simple, entire and alternate; the flowers are regular, usually with 3 sepals and 6 petals, the latter brown or tawny yellow, not showy; the stamens numerous; and the fruit an aggregation of berries (syncarp) in which the seeds are embedded or dry or capsular. Many species are grown for their edible fruits, for perfume, and for ornament. A few extend into temperate regions, as the North American pawpaw (*Asimina triloba*), found northward to New York and Michigan. Many valuable fruits belong to the genus *Anona*; among these are the cherimoya (*A. Cherimola*), of the American tropics, now cultivated in the southern United States; the custard-apple or bullock's-heart (*A. reticulata*), of tropical America; the sugar-apple, sweet-sop or ate (*A. squamosa*), cultivated throughout the Tropics; the soursop or Guanábana (*A. muricata*); widely grown in tropical lands; the ilama (*A. diversifolia*) of Mexico and Guatemala; the alligator-apple, or cork-wood (*A. glabra*), of tropical America; and the posh-té (*A. scleroderma*), of Guatemala and Mexico. The biribá (*Rollinsia deliciosa*) and related species are highly esteemed fruits from Brazil to Central America. A tree (*Porcelia Saffordiana*), recently discovered in Bolivia, bears immense fruits sometimes attaining 40 lb. weight. The ylang-ylang (*Cananga odorata*), native to the East Indies, is the source of the famous perfume of Malaysia and the Philippines. The exceedingly fragrant climbing ylang-ylang (*Artabotrys odoratissima*), native to India, China and the Philippines, is sparingly planted in southern Florida. (See CHERIMOYA; CUSTARD-APPLE; SWEET-SOP.)

**APOCYNACEAE**, the dog-bane family, a numerous group of dicotyledonous plants, composed chiefly of tropical twining shrubs but including also various trees and perennial herbs, all with a milky often poisonous juice. The leaves are simple, entire and usually opposite; the flowers are regular, sympetalous, with the parts in fours or fives and are borne either singly or clustered in cymes or panicles. The anthers are arrow-shaped and pointed, and the granular pollen is often glutinous; the ovary is mostly superior, with two or more carpels. There are about 180 genera and 1,400 species, comparatively few of which are found in cool temperate regions. In the British Isles the family is represented by the greater and the lesserperiwinkle (*Vinca major* and *V. minor*), the latter of which has run wild in the eastern United States. Of some 60 species representing the family in North America, only about six are found as far north as New York and adjacent Canada. The best known of these are the American dog-bane (*Apocynum androsaemifolium*) and the Indian hemp (*A. cannabinum*). Several tropical genera yield rubber (*Landlophia*, *Cardopinus*, *Funtumia*, *Urceola*, *Willoughbya*, etc.); others are source of drugs (*Aspidosperma*, *Strophanthus*, *Alstonia*, *Allamanda*, etc.). Some are exceedingly poisonous, notably the ordeal-tree (*Tanghinia*), of Madagascar; the manghas-tree (*Cerbera*), of tropical Asia; and the Bushman's poison (*Acocanthera*), of South Africa. Other widely known plants of this family are the oleander (*Nerium oleander*); the temple-tree or frangipani (*Plumeria acuminata*); the crape-jasmine (*Tabermontanae coronaria*); the star-jasmine (*Trachelospermum jasminoides*); and the Chilean jasmine (*Mandevilla suaveolens*). The Natal-plum (*Carissa grandiflora*) and several other species produce edible fruits and many are showy ornamental plants. (See DOG-BANE; INDIAN HEMP.)



A VERTICAL SECTION THROUGH THE FLOWERING RUSH AND ITS FLORAL DIAGRAM



THE WATER PLANTAIN, THE COMMON REPRESENTATIVE OF THE ALISMACEAE FAMILY IN GREAT BRITAIN. Upper left, the flower enlarged. Upper right, its floral diagram. Lower left, vertical section through flower. Lower right, the fruit



## PUBLISHERS' NOTE

Since the publication of the New 14th Edition of the Encyclopaedia Britannica, we have received thousands of requests to publish in separate form the articles in certain fields of knowledge so that these articles may be the more available for continuous reading, for students' use, etc. Accordingly we have prepared booklets containing all the Britannica articles on Painting; Mammals and Birds; Chinese Art; Botany: Plants and Gardening; Botany, the Science; The Earth, the Seas and the Heavens; Japanese Art; Fishes, Reptiles and Insects; The Theatre and Motion Pictures; Graphic Arts; and expect to follow these with many others. We trust they will prove useful, not only in themselves but also as evidence of the wide scope and the fullness of information in the Britannica itself.

The articles in this booklet are all taken *verbatim* from the New 14th Edition of the Encyclopaedia Britannica except that material not essential to the subject has been omitted and in a few unimportant instances certain material has been condensed for mechanical reasons. The plates, too, are reproduced unchanged but the numbering is not always consecutive because the original numbering has been retained in order to agree with the text. A number of cross references to articles not in this booklet have also been retained for the benefit of those who possess the Britannica.

Following the Britannica custom, we have retained at the end of signed articles, the initials and not the full name of the author. The reader, however, can always identify the author by referring to the List of Contributors where the full names of the authors are given together with their initials.

**AQUIFOLIACEAE**, a family of trees and shrubs, the best-known members of which are the holly (*q.v.*) and the Paraguayan tea, both of the genus *Ilex*.

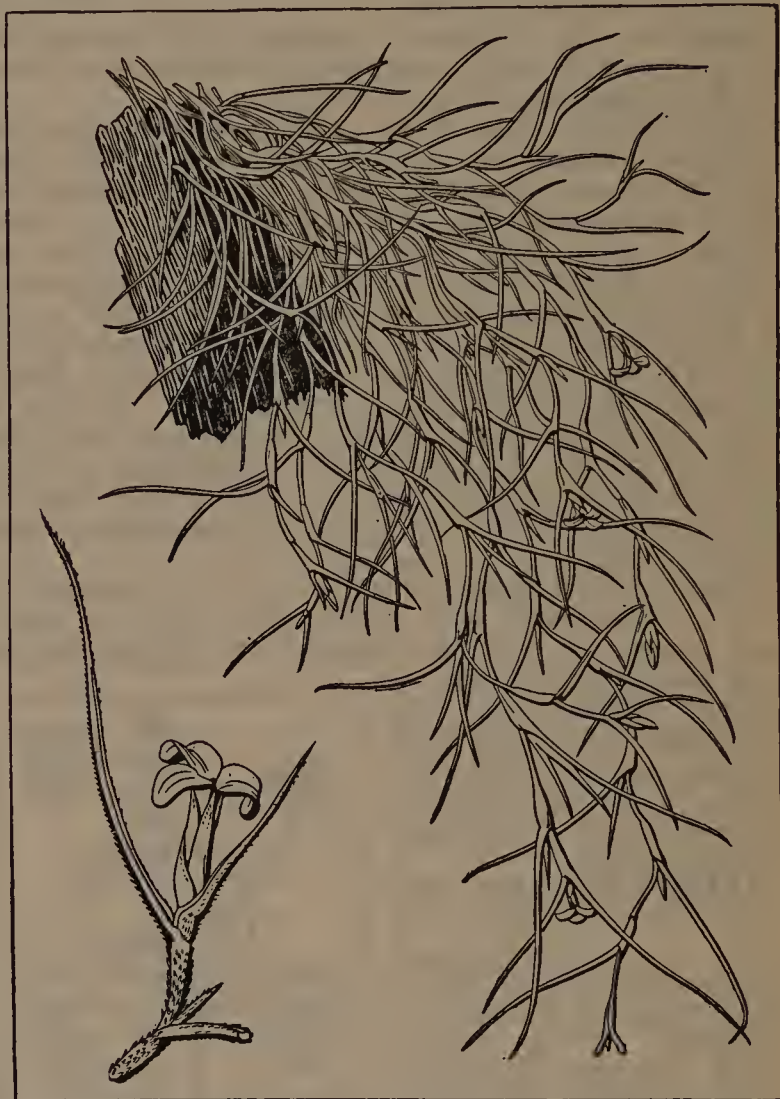
**ASCLEPIADACEAE**, the milkweed family, a distinctly marked group of dicotyledonous plants comprised chiefly of shrubs and woody vines, though many are perennial herbs, mostly with a milky juice. Like the Apocynaceae (*q.v.*), to which they are closely related, most of the species, about 1,700 in number and divided into some 320 genera, are tropical. The continent of Africa is the headquarters of the family. The flowers are regular, sympetalous and usually arranged in umbels, though sometimes in cymes or racemes; the fruit from each flower consists of a pair of more or less fleshy pods containing numerous seeds which are usually appendaged with a long tuft of hairs. As regards forms and habits of growth, the Asclepiadaceae ranks among the most unusual of plant families. Many are rope-like lianas of equatorial forests. Others are epiphytes with greatly modified leaves, which, in some species, take the form of pitchers for holding water. Certain South African species are fleshy, cactus-like plants. Still others form a cluster of leafless, whip-like stems. In some species the stems develop tuberous bases in which water is stored.

Although the family contains no economic plants of the first rank, numerous species are useful. Many are of value medicinally; the milky juice of the so-called cow-plant (*Gymnena lactiferum*), of Ceylon, is edible as is that of its South African counterpart (*Oxystelma esculentum*), and the tender shoots of various species are eaten as salads and pot herbs. Others are dye-plants, as, for example, *Marsdenia tinctorium*; various species produce caoutchouc, and others yield bast fibres. The juice of *Gonolobus* is used for poisoning arrows, and that of *Cynanchum* for poisoning fish. A large number are cultivated as ornamental plants, among which are the mosquito plant (*Cynanchum*), the silk-vine (*Periploca graeca*), the carrion-flower (*Stapelia variegata*), and the fragrant wax-plant (*Hoya carnosa*) and stephanotis (*S. floribunda*). The

madar or oschur (*Calotropis procera*), native to southwestern Asia, is believed to be the sodom apple mentioned in the Bible; the bark of the Indian madar (*C. gigantea*) yields a fibre and the seeds a floss.

Of some 80 representatives of the family native to the United States and Canada, the most common and conspicuous are the milkweeds (*Asclepias*). Among the best-known of these are the butterfly-weed (*q.v.*) and the swamp milkweed (*A. incarnata*), both with showy, handsome flowers. The blood-flower (*A. curassavica*), native to tropical America, and frequently grown in green-houses, has become naturalized in the southern United States. (See MILKWEED.)

**BROMELIACEAE**, in botany, a family of Monocotyledons, confined to tropical and sub-tropical America; it consists of about 65 genera and 850 species. It includes the pineapple (*q.v.*) and



FROM "CURTIS' BOTANICAL MAGAZINE," BY PERMISSION OF THE ROYAL HORTICULTURE SOCIETY  
SLENDER HANGING BRANCHES OF SPANISH MOSS, A PERCHING PLANT WHICH HANGS IN FESTOONS FROM TREES IN THE SOUTHERN UNITED STATES AND TROPICAL AMERICA

also the so-called Spanish moss, a rootless plant, which hangs in long grey lichen-like festoons from the branches of trees, a native of Mexico and the southern United States; the water required is absorbed from the moisture in the air by peculiar hairs which cover the surface of the shoots. The plants are generally herbs with a shortened stem bearing a rosette of leaves and a spike or panicle of flowers. They are dry-country plants (xerophytes); the narrow leaves are protected by a thick cuticle, and have a sheath which embraces the stem and forms, with the sheaths of the other leaves of the rosette, a basin in which water collects, with fragments of rotting leaves and the like. Peculiar hairs are developed on the inner surface of the sheath by which the water and dissolved substances are absorbed. The leaf-margins are often spiny, and the leaf-spines of *Puya Chilensis* are used by the natives as fish-hooks. Several species are grown as hot-house plants for the bright colour of their flowers or flower-bracts, e.g., species of *Tillandsia*, *Billbergia*, *Aechmea*.



**CAPRIFOLIACEAE**, a family of shrubs and trees, characterized by having the petals of the flower united. The plants are sympetalous Dicotyledons; common representatives are *Sambucus* (elder), *Viburnum* (guelder-rose and wayfaring tree), *Lonicera* (see HONEYSUCKLE); *Adoxa* (moschatel), a small herb with a creeping stem and small yellowish-green flowers, is occasionally found on damp hedge-banks; *Linnaea*, a slender creeping evergreen with a thread-like stem and pink bell-shaped flower, a northern plant, occurs in cold woods and mountains of Asia, Europe and North America. The leaves are opposite, simple as in honeysuckle, or compound as in elder; they have usually no stipules.



FROM "CURTIS' BOTANICAL MAGAZINE," BY PERMISSION OF THE ROYAL HORTICULTURE SOCIETY  
FLOWERING BRANCH OF GUELDER ROSE (*VIBURNUM OPULUS*) SHOWING THE STERILE OUTER FLOWERS WITH LARGE COROLLAS  
Attractive to insects which pollinate the fertile inner flowers with reduced corollas

The flowers are regular as in *Viburnum* and *Sambucus*, more rarely two-lipped as in *Lonicera*; the sepals and petals are usually five in number and placed above the ovary, the five stamens are attached to the corolla-tube, there are three to five carpels, and the fruit is a berry as in honeysuckle or snowberry (*Symphoricarpus*), or a stone fruit, with several, usually three, stones, as in *Sambucus*.

In *Sambucus* and *Viburnum* the small white flowers are massed in heads; honey is secreted at the base of the styles and, the tube of the flower being very short, is exposed to the visits of flies and insects with short probosces. The flowers of *Lonicera*, which have a long tube, open in the evening, when they are sweet-scented and are visited by hawk-moths. The family contains about 300 species, chiefly natives of the north temperate zone and the mountains of the tropics. Several genera afford ornamental plants; such are *Lonicera*, erect shrubs or twiners with long-tubed white, yellow or red flowers; *Symphoricarpus*, a North American shrub, with small whitish pendulous flowers and white berries; *Diervilla* (also known as *Weigelia*), and *Viburnum*, including *V. Opulus*, guelder rose, in the cultivated forms of which the corolla has become enlarged at the expense of the essential organs and the flowers are neuter.

The family is more abundant in the eastern part of North America than in the western mountain region, the large genera being honeysuckle (*Lonicera*) and arrow-wood (*Viburnum*).

**CARYOPHYLLACEAE**, a family of dicotyledonous plants, containing about 80 genera with 1,300 species, and widely distributed, especially in temperate, alpine and Arctic regions. The plants are herbs, sometimes becoming shrubby at the base, with opposite, simple, generally uncut leaves and swollen nodes. The main axis ends in a flower (definite inflorescence), and flower-bearing branches are borne one on each side by which the branching is often continued. The flowers are regular, with four or five sepals which are free or joined to form a tube in their lower portion, the same number of petals, free and springing from below the ovary, twice as many stamens, inserted with the petals, and a pistil of two to five carpels joined to form an ovary containing a large number of ovules on a central placenta and bearing two to

five styles; the ovary is one-celled or incompletely partitioned at the base into three to five cells; honey is secreted at the base of the stamens. The fruit is a capsule containing a large



FIG. 1.—PINK (*DIANTHUS*), A SWEET SCENTED FLOWER OF RED OR PINK AND WHITE BLOSSOMS

number of small seeds and opening by apical teeth; the seed contains a floury endosperm and a curved embryo.

The family is divided into two well-defined tribes which are



FIG. 2.—PINK (*DIANTHUS*), SHOWING DETAILS OF STRUCTURE

- A. Flowering shoot
- B. Flower in vertical section
- C. Floral diagram

distinguished by the character of the flower and the arrangements for ensuring pollination.

I. *Alsinoideae*: the sepals are free and the flowers are open,



with spreading petals, and the honey which is secreted at the base of the stamens is exposed to the visits of short-tongued insects, such as flies and small bees; the petals are white in colour. It includes several British genera, *Cerastium* (mouse-ear chickweed), *Stellaria* (stitchwort and chickweed), *Arenaria* (sandwort), *Sagina* (pearlwort), *Spergula* (spurrey) and *Spergularia* (sandwort spurrey).

II. *Silenoideae*: the sepals are joined below to form a narrow tube, in which stand the long claws of the petals and the stamens, partly closing the tube and rendering the honey inaccessible to all but long-tongued insects such as the larger bees and Lepidoptera. The flowers are often red. It includes several British genera:—*Dianthus* (pink), *Silene* (catchfly, bladder campion), *Lychnis* (campion, *L. Flos-Cuculi* is ragged robin), and *Githago* or *Agrostemma* (corn cockle). Several, such as *Lychnis vespertina*, *Silene nutans* and others, open their flowers and become scented in the evening or at night, when they are visited by night-flying moths.

In North America the family is represented by about 300 species, most numerous in mountain regions and belonging chiefly to *Silene*, *Arenaria*, *Alsine* and *Cerastium*.

The plants of this family are of little or no economic value. *Dianthus* (carnation and pink), *Gypsophila*, *Lychnis* and others, are garden plants.

**CHIMAERA.** This term is used in botany to apply to certain types of plants formerly known as "graft-hybrids." The term graft-hybrid suggests a plant which is a true hybrid produced by grafting, i.e., a plant produced by the fusion of cells derived respectively from the two plants grafted together. Such a union of cells would be of the nature of fertilization (see CYTOLOGY) and the offspring, having the characteristics of the two plants grafted, i.e., the stock and scion, would be of composite origin and so might properly be called a graft-hybrid. The development of a hybrid plant in such a way is, however, entirely unknown. It is true that plants composite in nature and having some of the characteristics of the two plants employed may develop from the graft, but they arise in an entirely different way without fusion of cells. The term graft-hybrid which used to be applied to them has therefore been dropped and they are now called "plant-chimaeras" or simply "chimaeras." A chimaera was a mythological monster of composite nature, having the head of a lion, the body of a goat and the tail of a dragon. The plant chimaeras are truly of composite nature and origin.

These chimaeras, though not under this name, have been known in gardens for some time, but it is only comparatively recently that their nature has been understood. In 1825 a French horticulturist grafted a shoot of *Cytisus purpureus* (the ordinary English broom, *Cytisus scoparius*, is an allied species) on the trunk of the ordinary laburnum, *Laburnum vulgare*. M. Adam was very surprised to find that a shoot developing at the graft was intermediate in character between the two parents or, rather, showed some characters of *C. purpureus* and others of *L. vulgare*.

The original composite plant has been propagated vegetatively and is fairly common in gardens, being usually called *Cytisus Adami* or *Laburnum Adami* after its producer. It was supposed to be a "graft-hybrid" as were also the so-called *Crataegomespilus* forms which arose at Bronveaux in Lorraine as a result of a graft between two different genera *Crataegus monogyna* and *Mespilus germanica*. In both cases it was observed that certain

shoots on the composite plant would revert or throw back to the original forms, i.e., to *L. vulgare* or *C. purpureus* in the one case or to *C. monogyna* or *M. germanica* in the other. Another supposed case of a graft hybrid was that of the Bizzaria orange which it was presumed had arisen from a graft between *Citrus aurantium* (the ordinary orange) and *C. media*.

### The Discovery of the Nature of "Graft-Hybrids."

—In 1907 our knowledge of this subject passed into a new phase. In that year H. Winkler published in Germany some experimental work on grafting *Solanum nigrum* (a common British plant with black berries sometimes known as black nightshade) as scion on *Solanum Lycopersicum* (the tomato) as stock. After the graft had taken, a transverse cut was made through it at the junction of the stems. From the surface of contact of the stock and scion a number of buds developed which grew out into new shoots. Most of these were just shoots of tomato or of nightshade, but one of them was composite in nature, having the characters of tomato on one

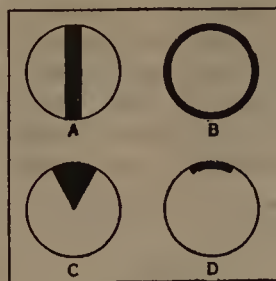


FIG. 3.—DETAIL OF THE MOUSE-EAR CHICKWEED (*CERASTIUM HIRSUTUM*)

A. Pistil cut vertically  
B. Pistil cut horizontally, and the halves separated so as to show the interior of the cavity of the ovary

### CHIMAERAS, PLANTS OF COMPOSITE NATURE AND ORIGIN

A. Cross section of grafted stock through point of union  
B. Periclinal chimaera  
C. and D. Sectorial chimaera. The portion in black represents the tissue of the scion and the unshaded portion the tissue of the stock

side and of nightshade on the other. Some of the leaves which arose at the junction of the two halves had partly the characters of one species and partly of the other. Winkler very appropriately termed this shoot a *chimaera* since it was half of one species and half of another. In 1908 Winkler published the results of an examination of 268 grafts, between the same two species, which bore more than 3,000 shoots when cut across in the way described. Of these, five were chimaeras of the kind described the year before, but one was intermediate between the stock and scion, being rather nearer to the nightshade than the tomato. This shoot Winkler believed to be a real "graft-hybrid" to which he gave the name *Solanum tubingenense* since it was produced at Tübingen. Next year he claimed to have produced several more graft-hybrids to which he gave special names, *S. Darwinianum*, *S. Gaertnerianum*, *S. proteus* and *S. Koelreuter*. It was found, however, that seedling plants (arising of course sexually from these forms) always reverted to the *nearer parent*, never producing hybrid seedlings. Again if the new forms were crossed with the *nearer parent* the product was always pure tomato or pure nightshade. This is not the behaviour which one would expect from a true hybrid.

**Work on Variegated Plants.**—In 1909 E. Baur published observations on variegated plants which shed a new light on the nature of the so-called graft-hybrids. It is well known that the garden geranium (really *Pelargonium zonale*) often shows leaves with a white margin. When examined microscopically it is found that there are two or three layers of colourless cells covering the internal green tissue, and these tissues are separated right up to the growing point so that the variegated *Pelargonium* plant body consists of a green core surrounded with a white sheath. To such a plant Baur gave the name *periclinal chimaera*, i.e., a chimaera in which one component invests the other. He further suggested that Winkler's so-called graft-hybrids between tomato and nightshade were also periclinal chimaeras, i.e., plants with a tomato sheath over a core of nightshade tissue or a sheath of nightshade over a core of tomato tissue. This would explain why these forms produce seedlings of either tomato or nightshade, since the sexual cells arise solely from the central tissue, the outer cells not being concerned. Baur also examined *Cytisus Adami* and the *Crataegomespilus* "hybrids" and found that they also were periclinal chimaeras. *Cytisus Adami* has a core or body of *Laburnum vulgare* with a skin (epidermis) of *Cytisus purpureus*. In the other case the chimaeras have either a *Crataegus* core with a *Mespilus* skin (epidermis), or vice versa. Winkler on examining his so-called *Solanum* "hybrids" in the light of Baur's suggestion found that Baur was correct in his surmise. *Solanum tubingenense* has a nightshade core and a tomato skin one layer thick. *S. proteus* has also a nightshade core and a tomato skin but the skin



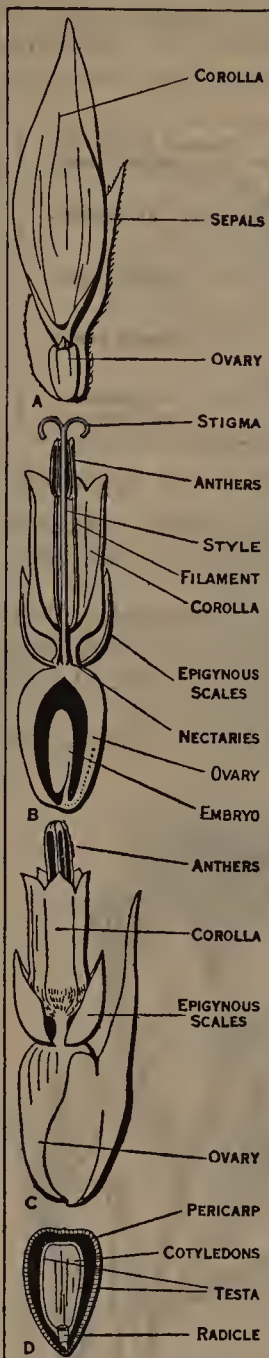
is thicker, having two layers. *S. Koelreuterianum* has a tomato core and a nightshade skin one layer thick.

**Classes of Chimaeras.**—Winkler produced his chimaeras experimentally by “cleft grafting” of main shoots, a tongue of the scion being inserted in a cleft in the stock. When the two shoots had united the graft was cut across transversely. The relation of parts would then be as shown in fig. 1a where the black area represents the scion and the light area the stock. The cut surface of the graft produces “callus” and from this buds develop. Most of these are “pure” in origin since they arise from callus tissue which has developed from either stock or scion; but some may arise from callus, which is partly of stock and partly of scion origin, and these may give chimaeras. The tissues in the shoots arising from the buds of mixed origin may be arranged as in fig. 1b, which is a *periclinal chimaera*, or as in fig. 1c, which is a *sectorial chimaera*, only a section of the tissue in cross-section (the black portion) being of scion nature. The first chimaera Winkler produced was of this type, though in that case the chimaera was a “half and half” one. The third type shown in fig. 1d was formerly considered as sectorial, but it is really an incomplete periclinal for which the term *mericlinal* has been suggested (see bibliography under Jorgensen and Crane). True sectorial chimaeras are very rare, the plant first obtained by Winkler being of this type, as are also a few *Pelargoniums*. The periclinal type is quite common, e.g., *Cytisus Adami*, the forms of *Crataegomespilus*, *Pelargonium*, *Bouvardia*. The chimaera may be a whole plant or a shoot only or only a smaller portion such as a flower or fruit. In plants such as *Bouvardia*, which is of the complete periclinal type, we have the interesting result that shoot cuttings and root cuttings produce plants of different types; in one case the new plant arises from one set of tissues, in the other case from the other set. It has recently been shown that chimaeras are more common than was suspected. The tubers of certain varieties of the common potato are shown to be chimaeras. If the shoots developing from the normal eyes are rubbed off, the new one developing arises from deeper tissues and so from the other component of the chimaera, thus giving shoots of a different type.

**BIBLIOGRAPHY.**—The literature of this subject is largely in German. H. Winkler, “Ueber Propfbastarde und pflanzliche Chimären,” *Berichte der deutsche botanische Gesellschaft* (1907); *ibid.* (1908); “Ueber das Wesen der Propfbastarde, Periklinalchimären, und Hyperchimären,” *ibid.* (1910). There is a good review of the literature up to 1911 in the *Botanical Gazette* (1911). For later papers in English, see W. Bateson, “Root Cuttings and Chimaeras,” *Journal of Genetics* (Cambridge, 1916 and 1921); C. A. Jorgensen and M. B. Crane, “Formation and Morphology of *Solanum* Chimaeras,” *ibid.* (1927). (V. H. B.)

**COMPOSITAE**, the name given to the largest family of flowering plants. It includes approximately 900 genera and over 13,000 species comprising about one-tenth of the flowering plants. It is characterized by the crowding of the flowers into heads. The family is cosmopolitan, and the plants show considerable variety in habit. The great majority, including most British representatives, are herbaceous, but in the warmer parts of the world shrubs and arborescent forms also occur; the latter are characteristic of the flora of oceanic islands. In herbaceous plants the leaves are often arranged in a rosette on a much shortened stem, as in dandelion, daisy and others; when the stem is elongated the leaves are generally alternate. The root is generally thickened, sometimes, as in dahlia, tuberous; root and stem contain oil passages, or, as in lettuce and dandelion, a milky white latex. The flowers are crowded in heads (*capitula*) which are surrounded by an involucre of green bracts,—these protect the head of flowers in the bud stage, performing the usual function of a calyx. The enlarged top of the axis, the receptacle, is flat, convex or conical, and the flowers open in centripetal succession. In many cases, as in the sunflower or daisy, the outer or ray-florets are larger and more conspicuous than the inner, or disc-florets; in other cases, as in dandelion, the florets are all alike. Ray-florets when present are usually pistillate, but neuter in some genera (as *Centaurea*); the disc-florets are hermaphrodite. The flower is epigynous; the calyx is sometimes absent, or is represented by a rim on the top of the ovary, or takes the

form of hairs or bristles which enlarge in the fruiting stage to form the pappus, by means of which the seed is dispersed. The



FROM PERCY GROOM, "ELEMENTARY BOTANY" (BELL & SONS)  
SUNFLOWER, SHOWING  
DETAILS OF STRUCTURE  
A. Ray flower, which has no stamens, style, or stigma  
B. Vertical section through an inner floret  
C. Inner floret; regular, with tubular five-toothed corolla, stamens and pistil  
D. Vertical section of the one seeded fruit

corolla, of five united petals, is regular and tubular in shape in the disc-florets, or irregular, when it is either strap-shaped (ligulate), as in the ray-florets of daisy, etc., or all the florets of dandelion, or more rarely two-lipped. The five stamens are attached to the interior of the corolla-tube; the filaments are free; the anthers are joined (syngenesious) to form a tube round the single style, which ends in a pair of stigmas. The inferior ovary contains one ovule (attached to the base of the chamber), and ripens to form a dry one-seeded fruit; the seed is filled with the straight embryo.

The flower-heads are an admirable example of an adaptation for pollination by insects. The crowding of the flowers in heads ensures the pollination of a large number as the result of a single insect visit. Honey is secreted at the base of the style, and is protected from rain or dew and the visits of short-lipped insects by the corolla-tube, the length of which is correlated with the length of proboscis of the visiting insect. When the flower opens, the two stigmas are pressed together below the tube formed by the anthers, the latter split on the inside, and the pollen fills the tube; the style gradually lengthens and carries the pollen out of the anther tube, and finally the stigmas spread and expose their receptive surface which has hitherto been hidden, the two being pressed together. Thus the life history of the flower falls into two stages, an earlier or male and a later or female. This favours cross-pollination as compared with self-pollination. In many cases there is a third stage, as in dandelion, where the stigmas finally curl back so that they touch any pollen grains which have been left on the style below, thus ensuring self-pollination if cross-pollination has not been effected.

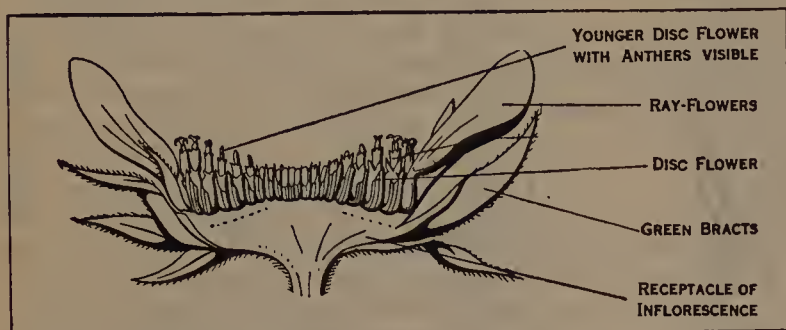
The devices for distribution of the fruit are very varied. Frequently there is a hairy or silky pappus forming a tuft of hairs, as in thistle or coltsfoot, or a parachute-like structure as in dandelion; these render the fruit sufficiently light to be carried by the wind. In *Bidens* the pappus consists of two or more stiff-barbed bristles which cause the fruit to cling to the coats of animals. Occasionally, as in sunflower or daisy, the fruits bear no special appendage and remain on the head until jerked off.

Compositae are generally considered to represent the most highly developed order of flowering plants. By the massing of the flowers in heads great economy is effected in the material required for one flower, as conspicuousness is ensured by the association; economy of time on the part of the pollinating insect is also effected, as a large number of flowers are visited at one time. The floral mechanism is both simple and effective, favouring cross-pollination, but ensuring self-pollination should that fail. The means of seed-distribution are also very effective.

A few members of the order are of economic value, e.g., *Lactuca* (lettuce; *q.v.*), *Cichorium* (chicory; *q.v.*), *Cynara* (artichoke and cardoon; *q.v.*), *Helianthus* (Jerusalem artichoke). Many are cultivated as garden or greenhouse plants, such as *Solidago* (golden rod), *Ageratum*, *Aster* (*q.v.*) (Michaelmas daisy), *Helichrysum* ("everlasting"), *Zinnia*, *Rudbeckia*, *Helianthus* (sun-



flower), *Coreopsis*, *Dahlia* (q.v.), *Tagetes* (French and African marigold), *Gaillardia*, *Achillea* (yarrow), *Chrysanthemum*, *Tanacetum* (tansy), *Arnica*, *Doronicum*, *Cineraria*, *Calendula* (common marigold), *Echinops* (globe thistle), *Centaurea* (q.v.). Some are of medicinal value, such as *Anthemis* (chamomile), *Artemisia*



FROM GROOM, "ELEMENTARY BOTANY" (BELL & SONS)

VERTICAL SECTION THROUGH THE FLOWER HEAD OF THE SUNFLOWER

(wormwood), *Tussilago* (coltsfoot), *Arnica*. Insect powder is prepared from species of *Pyrethrum* now included in the genus *Chrysanthemum*.

The order is divided into two subfamilies:—*Tubuliflorae*, characterized by absence of latex, and the florets of the disc being not ligulate, and *Liguliflorae*, characterized by presence of latex and all the florets being ligulate. The first subfamily contains the majority of the genera, and is divided into a number of tribes. The family is well represented in Britain, in which 42 of the 900 genera are native. These include some of the commonest weeds, such as dandelion (*Taraxacum officinale*), daisy (*Bellis perennis*), groundsel (*Senecio vulgaris*) and ragwort (*S. Jacobaea*); coltsfoot (*Tussilago Farfara*) is one of the earliest plants to flower, and other genera are *Chrysanthemum* (ox-eye daisy and corn-marigold), *Arc-tium* (burdock), *Centaurea* (knapweed and cornflower), *Carduus* and *Cnicus* (thistles), *Hieracium* (hawkweed), *Sonchus* (sow-thistle), *Achillea* (yarrow, or milfoil, and sneezewort), *Eupatorium* (hemp-agrimony), *Gnaphalium* (cud-weed), *Erigeron* (fleabane), *Solidago* (golden-rod), *Anthemis* (may-weed and chamomile), *Cichorium* (chicory), *Lapsana* (nipplewort), *Crepis* (hawk's-beard), *Hypochaeris* (cat's-ear), and *Tragopogon* (goat's beard).

In North America over 200 genera are represented by many species distributed over the whole country.

**CONVOLVULACEAE**, a botanical family belonging to the tube-flowered series of the group of Dicotyledons having joined petals. It contains about 50 genera with more than 1,000 species, and is found in all parts of the world except the coldest, but is best developed in tropical Asia and tropical America. The most characteristic are twining plants with generally smooth heart-shaped leaves and large showy white or purple flowers, as, for instance, the greater bindweed of English hedges, *Calystegia sepium*, and many species of the genus *Ipomoea*, the largest of the family including the "convolvulus major" of gardens, and morning glory. The creeping or trailing type is common, as in the English bindweed (*Convolvulus arvensis*), which has also a tendency to climb, and *Calystegia Soldanella*, the sea-bindweed, the long creeping stem of which forms a sand-binder on temperate seashores; a widespread and efficient tropical sand-binder is *Ipomoea Pes-Caprae*. In hot dry districts such as Arabia and north-east tropical Africa, genera have been developed with a low, much-branched,

dense, shrubby habit, with small hairy leaves and very small flowers. An exceptional type is represented by *Humbertia*, a native of Madagascar, which forms a large tree; the dodder (q.v.) is a genus (*Cuscuta*) of leafless parasites with slender thread-like twining stems. The flowers stand singly in the leaf-axils or form cymose



HEDGE BINDWEED (*CALYSTEGIA SEPIUM*), A TWINING PLANT COMMON IN TEMPERATE REGIONS, SOMETIMES GROWN AS A TRELLIS VINE

inflorescences; they are sometimes crowded into small heads. The bracts are usually scale-like, but sometimes foliaceous, e.g., *Calystegia*, where they are large and envelop the calyx. In North America, much the largest genera are *Ipomoea* (morning glory), *Cuscuta* (dodder, love vine) and *Convolvulus* (bindweed).



BY COURTESY OF THE WILD FLOWER PRESERVATION SOCIETY

CREeping BINDWEED (*CONVOLVULUS ARVENSIS*), A WIDESPREAD WEED WITH PROSTRATE OR ASCENDING STEMS AND WHITE FLOWERS

petals and alternating with five non-striated weaker triangular areas. The slender filaments of the stamens vary widely, often in the same flower; the anthers are linear to ovate in shape, attached at the back to the filament and open lengthwise. The ovary is generally two-chambered, with two inverted ovules standing side by side at the inner angle of each chamber. The style is simple or branched, and the stigma linear, capitate or globose. The fruit is usually a capsule opening by valves; the seeds, where four are developed, are each shaped like the quadrant of a sphere; the seed-coat is smooth, warty or hairy; the embryo is large with generally broad cotyledons surrounded by a horny endosperm. *Cuscuta* has a thread-like spirally twisted embryo with no trace of cotyledons.

The large showy flowers are visited by insects for the honey secreted by a ring-like disk below the ovary; large-flowered species of *Ipomoea* with narrow tubes are adapted for the visits of birds.

The largest genus, *Ipomoea*, has about 400 species distributed throughout the warmer parts of the earth. *Convolvulus* has about 150 species, mainly in temperate climates. *Cuscuta* contains nearly 100 species in the warmer and temperate regions; two are British.

The tubers of *Ipomoea Batatas* are rich in starch and sugar, and, as the "sweet potato," form one of the most widely distributed foods in the warmer parts of the earth. Several species are used medicinally for the strong purging properties of the milky juice they contain; jalap is the product of the tubercles of *I. Purga*, a



native of Mexico. The resinous cathartic scammony is obtained from the roots of *Convolvulus Scammonia*, native to Asia Minor. Species of *Ipomoea* (morning glory), *Convolvulus* and *Calystegia* are cultivated as ornamental plants. *Calystegia lepium* and *Convolvulus arvensis* (bindweed) are pests in fields and gardens and many of the dodders (*Cuscuta*) cause damage to crops.

**CRASSULACEAE**, in botany, a family of dicotyledons, containing 25 genera and 450 species; of cosmopolitan distribution, but most developed in South Africa. The plants are herbs or small shrubs, generally with thick fleshy stems and leaves, adapted for life in dry, especially rocky places. The fleshy leaves are often reduced to a more or less cylindrical structure, as in the stone-crops (*Sedum*), or form closely crowded rosettes as in the house-leek (*Sempervivum*). Correlated with their life in dry situations, the bulk of the tissue is succulent, forming a water-store, which is protected from loss by evaporation by a thickly cuticularized epidermis covered with a waxy secretion which gives a glaucous appearance to the plant. The flowers are generally arranged in terminal or axillary clusters, and are markedly regular with the same number of parts in each series. This number is, however, very variable, and often not constant in one and the same species. The sepals and petals are free or more or less united, the stamens as many or twice as many as the petals; the carpels, usually free, are equal to the petals in number, and form in the fruit follicles with two or more seeds. The means of vegetative propagation are general. Many species spread by means of a creeping much-branched rootstock or, as in house-leek, by runners that perish after producing a terminal leaf-rosette. In other cases small portions of the stem or leaves give rise to new plants by budding, as in *Bryophyllum*, where buds develop at the edges of the leaf and form new plants.

The family is almost absent from Australia and Polynesia, and has but few representatives in South America; it is otherwise generally distributed. The largest genus, *Sedum*, contains about 150 species in the temperate and colder parts of the northern hemisphere; nine occur wild in Britain, including *S. Telephium* (orpine) and *S. acre* (common stonecrop). The species are very easily cultivated and will thrive in almost any soil. *Crassula* has about 150 species, chiefly at the Cape. *Cotyledon*, a widely distributed genus with about 100 species, is represented in the British Isles by *C. umbilicus*, pennywort, or navelwort, which takes its name from the succulent peltate leaves. It grows profusely on dry rocks and walls, especially on the western coasts, and bears a spike of drooping greenish cup-shaped flowers. The *Echeveria* of gardens is included in this genus. *Sempervivum* has about 50 species in the mountains of central and southern Europe, in the Himalayas, Abyssinia and the Canaries and Madeira; *S. tectorum*, common house-leek, is seen often growing on tops of walls and house-roofs. The hardy species will grow well in dry sandy soil, and are suitable for rockeries, old walls or edgings.

In North America some 40 representatives of the family are found, most numerous from the Rocky Mountains westward, 20 occurring in California, mostly species of *Sedum* and *Cotyledon*.

The family is closely allied to Saxifragaceae, from which it is distinguished by its fleshy habit and the larger number of carpels.

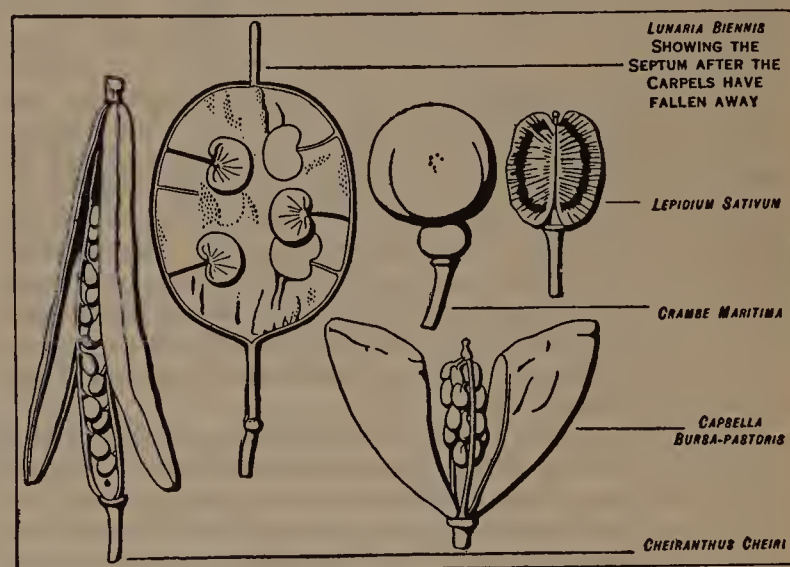
**CRUCIFERAE**, a family of flowering plants, which derives its name from the cruciform arrangement of the four petals of the

flower. It is a family of herbaceous dicotyledons, many of which, such as wallflower, stock, mustard, cabbage, radish and others, are well-known garden or field-plants. Many are annuals; among these are some of the commonest weeds of cultivation, shepherd's purse



FIG. 1.—WALLFLOWER (*CHEIRANTHUS CHEIRI*), A HARDY PERENNIAL NATIVE TO SOUTHERN EUROPE, LONG A GARDEN FAVOURITE. A. FLOWER OF THE WALL-FLOWER IN VERTICAL SECTION. B. FLORAL DIAGRAM OF WINTER CRESS (*BARBAREA VULGARIS*)

(*Capsella Bursa-pastoris*), charlock (*Brassica Sinapis*), hedge mustard (*Sisymbrium officinale*), Jack-by-the-hedge (*S. Alliaria*). Others are biennials producing a number of leaves on a short stem in the first year, and in the second sending up a flowering shoot at the expense of the nourishment stored in the thick tap-root during the previous season. Under cultivation this root becomes much



AFTER BAILLON, "HISTOIRE DES PLANTES"

FIG. 2.—DETAILS OF THE FRUITS PRODUCED BY CRUCIFEROUS PLANTS. The Cruciferae include among other members the radish, turnip, cauliflower, watercress, wallflower, sweet alyssum, wild mustard and pepper grass

enlarged, as in turnip, swede and others. Wallflower (*Cheiranthus cheiri*), however, is a perennial. The leaves when borne on an elongated stem are arranged alternately and have no stipules. The flowers are in racemes without bracts; during the life of the flower its stalk continues to grow so that the open flowers of an inflorescence stand on a level (that is, are corymbose). The flowers are regular, with four free sepals arranged in two pairs at right angles, four petals arranged crosswise in one series, and two sets



of stamens, an outer with two members and an inner with four, in two pairs placed in the middle line of the flower and at right angles to the outer series. The four inner stamens are longer than the two outer; and the stamens are hence collectively described as tetradynamous. The pistil, which is above the rest of the members of the flower, consists of two carpels joined at their edges to form the ovary which becomes two-celled by subsequent ingrowth of a septum from these united edges; a row of ovules springs from each edge. The fruit is a pod or siliqua splitting by two valves from below upwards and leaving the placentas with the seeds attached to the *replum* or framework of the septum. The seeds are filled with the large embryo, the two cotyledons of which are variously folded. In germination the cotyledons come above ground and form the first green leaves of the plant.

Pollination is effected by insects. The petals are generally white or yellow, more rarely lilac or some other colour, and between the bases of the stamens are honey-glands.

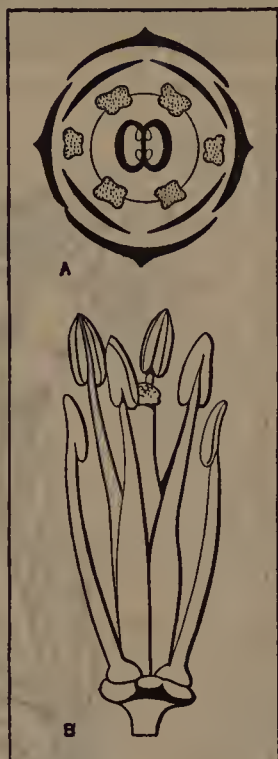
Cruciferae is a large family containing 220 genera and about 1,900 species. It has a world-wide distribution, but finds its chief development in the temperate and frigid zones, especially of the northern hemisphere, and as Alpine plants. In the subdivision of the family into tribes use is made of differences in the form of the fruit and the manner of folding of the embryo. When the fruit is several times longer than broad it is known as a siliqua, as in stock; when about as long as broad, a silicula, as in shepherd's purse.

The family is well represented in Britain—among others by *Nasturtium* (*N. officinale*, water-cress), *Arabis* (rock-cress), *Cardamine* (bitter-cress), *Sisymbrium* (hedge mustard), etc.; *S. Irio* is London rocket (so-called because it sprang up after the fire of London in 1666), *Brassica* (cabbage and mustard), *Diplotaxis* (rocket), *Cochlearia* (scurvy-grass), *Capsella* (shepherd's purse), *Lepidium* (cress), *Thlaspi* (penny-cress), *Cakile* (sea rocket), *Raphanus* (radish), and others. Of economic importance are species of *Brassica*, including mustard (*B. nigra*), white mustard, used when young in salads (*B. alba*), cabbage (*q.v.*) and its numerous forms derived from *B. oleracea*, turnip (*B. campestris*), and swede (*B. Napus*), *Raphanus sativus* (radish), *Cochlearia Armoracia* (horse-radish), *Nasturtium officinale* (water-cress), *Lepidium sativum* (garden cress). *Isatis* affords a blue dye, woad. Many of the genera are known as ornamental garden plants; such are *Cheiranthus* (wallflower), *Matthiola* (stock), *Iberis* (candy-tuft), *Alyssum* (Alison), *Hesperis* (dame's violet), *Lunaria* (honesty) *Aubrietia* and others.

In North America the family is represented by about 50 genera, many of the species having been introduced from Europe as weeds, which have become distributed over a wide territory. In the eastern region the largest genera are rock cress (*Arabis*) and bitter cress (*Cardamine*); while in the western mountain region the largest genus is Whitlow-grass (*Draba*).

**CUCURBITACEAE**, a botanical family of dicotyledons, containing 90 genera and about 750 species, found in the temperate and warmer parts of the earth but especially developed in the tropics. The plants are generally annual herbs, climbing by means of tendrils and having a rapid growth. The long-stalked leaves are arranged alternately, and are generally palmately lobed and veined. The flowers or inflorescences are borne in the leaf-axils, in which a vegetative bud is also found, and at the side of the leaf-stalk is a simple or branched tendril. There has been much difference of opinion as to what member or members the tendril represents; the one which seems most in accordance with

facts regards the tendril as a shoot, the lower portion representing the stem, the upper twining portion a leaf. The flowers are unisexual, and markedly epigynous, the perianth and stamens being attached to a bell-shaped prolongation of the receptacle above the ovary. The five narrow pointed sepals are followed by five petals which are generally united to form a more or less bell-shaped



AFTER BAILLON, "HISTOIRE DES PLANTES"

FIG. 3.—CRUCIFERAE  
A. Floral diagram (*Brassica*)  
B. *Cardamine pratensis*.  
Flower with floral  
leaves removed

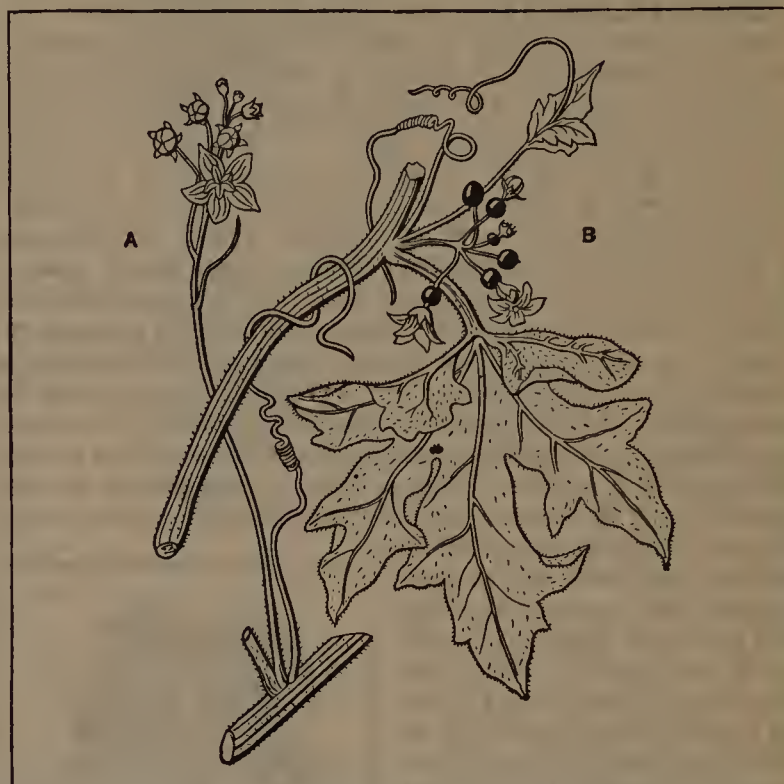


FIG. 1.—BRYONY. A HEDGE-CLIMBER WHICH BEARS SMALL GREENISH FLOWERS AND RED BERRIES

A. Male flowers. B. Female flowers

corolla. There are five stamens in the male flowers; the anthers open towards the outside, are one-celled, with the pollen-sacs often elaborately twisted and variously united. The carpels, normally three in number, form an ovary with three thick, fleshy, bifid placentas bearing a large number of ovules on each side, and generally filling the interior of the ovary with a juicy mass. The short thick style has generally three branches, each bearing a fleshy, usually forked stigma. The fruit is a fleshy many-seeded berry with a tough rind (*pepo*), and often attains considerable size. The embryo completely fills the seed.



FIG. 2.—MELON. AN EDIBLE MEMBER OF THE GOURD FAMILY, SHOWING FLOWERS AND FRUIT (PEPO) AND GENERAL HABIT OF GROWTH

The family is represented in Britain by bryony (*Bryonia dioica*), (fig. 1) a hedge-climber, perennial by means of large fleshy tubers which send up each year a number of slender angular stems. The leaves are heart-shaped with wavy margined lobes. The flowers are greenish,  $\frac{1}{2}$  to  $\frac{3}{4}$  in. in diameter; the fruit, a red several-seeded berry, is about  $\frac{1}{4}$  in. in diameter.

In North America the family is represented by a few genera comprising about 40 species, which occur chiefly in the southern parts of the United States and Mexico. Among these are the climbing wild cucumber or balsam apple (*Echinocystis lobata*)



and the star-cucumber (*Sicyos angulatus*), of the eastern United States and Canada; the calabazilla or mock orange (*Cucurbita foetidissima*), of the southwestern United States and Mexico; and the man-root (*Echinocystis fabacea*), of California.

Many genera are of economic importance; *Cucumis* affords cucumber (*q.v.*) and melon (*q.v.*); *Cucurbita*, pumpkin and marrow; *Citrullus vulgaris* is water-melon, and *C. Colocynthis*, colocynth; *Ecballium Elaterium* (squirting cucumber), ejects its seeds, with a watery fluid, by the contraction of the wall of the fruit; *Sechium edule* (chocho), a tropical American species, is cultivated for its edible fruit; it contains one large seed which germinates *in situ*. *Lagenaria* is the gourd (*q.v.*). The fruits of *Luffa cylindrica* have closely netted vascular bundles in the pericarp, forming a kind of loose felt which supplies the well-known loofah or bath-sponge.

**CUPRESSACEAE:** see GYMNOSPERMS.

**CUPULIFERAE**, a group name used to include two families of familiar trees (Fagaceae and Betulaceae), which resemble one another in many features. The plants are trees or shrubs with simple leaves alternately arranged and small unisexual flowers generally arranged in catkins and pollinated by wind-agency. The generally one-seeded nut-like fruit is associated with the persistent often hardened or greatly enlarged bracts forming the so-called cupule which gives the name to the group.



FIG. 1.—*CAREX RIPARIA*, THE LARGEST BRITISH SEDGE, FROM 3 TO 5 FT. HIGH

A. Male flower (Enlarged)

B. Female flower (Enlarged)

**CYCADALES:** see GYMNOSPERMS.

**CYCADS:** see GYMNOSPERMS.

**CYPERACEAE**, in botany, a family of monocotyledons. They are grass-like herbs, sometimes annual, but more often persisting by means of an underground stem, from which spring erect solitary or clustered, generally three-sided aerial stems, with leaves in three rows. The minute flowers are arranged in spikelets somewhat as in grasses, and these again in larger spike-like or paniced inflorescences. The flower has in rare cases a perianth of six scale-like leaves arranged in two whorls, and thus conforming to the common monocotyledonous type of flower. Generally the perianth is represented by hairs, bristles or similar developments, often indefinite in number; in the two largest genera, *Cyperus*, and *Carex* the flowers are naked. In a few cases there are two whorls of stamens, with three members in each; but generally only three at present; the pistil consists of two or three carpels, united to form an ovary bearing a corresponding number of styles and containing one ovule. The flowers, often



FIG. 1A.—*CAREX AMPULLACEA*, WHICH GROWS FROM 1 TO 3 FT. HIGH, IN BOGS AND MARSHES IN PARTS OF EUROPE, ASIA AND NORTH AMERICA

unisexual, are wind-pollinated. The fruit is one-seeded, with a tough, leathery or hard wall. There are 85 genera containing about 3,200 species and widely distributed throughout the earth, chiefly as marsh-plants. In the Arctic zone they form 10% of the flora. They will flourish in soils rich in humus which are too acid to support grasses. The large genus *Cyperus* contains about 600 species, chiefly in the warmer parts of the earth; *C. papyrus* is the Egyptian papyrus. *Carex*, the largest genus of the order,



FIG. 2.—A. A FLOWER CLUSTER OF COTTON-GRASS (*ERIOPHORUM POLYSTACHION*), ABOUT 2/3 NATURAL SIZE, FOUND WIDELY IN MARSHY LANDS. B. FLOWER OF THE TRUE BULRUSH (*SCIRPUS LACUSTRIS*), FROM WHICH MATS AND CHAIR BOTTOMS ARE MADE

the sedges, is widely distributed in the temperate, alpine and Arctic regions of both hemispheres containing over 1,000 species. It is represented by 60 species in Britain, and by over 200 species in North America. *Carex arenaria*, the sea-bent, grows on sand dunes and helps to bind the sand with its long cord-like underground stem which branches widely. *Scirpus lacustris*, the common bulrush, occurs in lakes, ditches and marshes; it has a spongy, green, cylindrical stem, reaching nearly an inch in thickness and 1 to 8 ft. high, which is usually leafless with a terminal branched inflorescence. *Eriophorum*, cotton-grass, is represented in Britain by several species in boggy land. They are small tufted herbs with cottony heads due to the numerous hair-like bristles which take the place of the perianth and become much elongated in the fruiting stage.

In North America, some species of *Carex* grow on dry land, but the largest ones occur in low grounds. They cover great areas of marsh land in the Upper Mississippi region, and are employed in the manufacture of "grass carpets."

**DIATOMACEAE:** see BACILLARIALES.

**DIOSCOREACEAE**, a family of monocotyledonous plants which includes the yam (*q.v.*), the black bryony (*Tamus communis*), and the elephant's-foot (*q.v.*). There are nine genera and about 220 species, all climbing herbs or shrubs with tubers



or rhizomes at the base. The flowers are usually regular, unisexual, inconspicuous; the parts are in threes.

**DIPSACACEAE**, a family of dicotyledonous plants, the best-known member of which is the teasel (*q.v.*). The family includes ten genera and 150 species. The scabiouses (*Scabiosa* *Knautia*) also belong to this family.

**DISTRIBUTION OF PLANTS:** see PLANTS: *Ecology and Distribution*.

**DROSERACEAE**, a family of dicotyledonous plants, remarkable in that all its members are insectivorous. There are five genera and about 100 species. *Drosera*, a cosmopolitan genus including about 90 species, has three British and seven North American representatives, known as sundews (*q.v.*). *Dionaea*, with a single species, is Venus' fly-trap (*q.v.*). *Aldrovanda*, also with only one species, is a water-plant, lacking roots.

**EBENACEAE**, a family of dicotyledonous trees and shrubs including the ebony (*q.v.*) and other valuable timber-trees. It has seven genera, with about 320 species, are chiefly tropical or subtropical, and especially abundant in Malaya. The fruit is usually a berry. The family is represented in the United States by two species of persimmon (*q.v.*).

**ECOLOGY OF PLANTS:** see PLANTS.

**EMPETRACEAE**, a family of dicotyledonous plants the best known member of which is the crowberry (*q.v.*). There are only four species, in three genera, confined to the northern hemisphere and the Andes. The parts of the flowers are in threes and the fruit is a drupe.

**EPACRIDACEAE**, a large family of dicotyledonous shrubs and trees, chiefly Australian, but also represented in India, New Zealand, South America and the Hawaiian islands. There are 30 genera and some 400 species. In Australia they fill the place occupied elsewhere by the Ericaceae (*q.v.*) or heath family. The flowers are usually white or red, symmetrical and pentamerous. The fruit is a capsule or a drupe. *Astroloma* is the Australian, *Lissanthe* the Tasmanian, cranberry. Species of *Epacris* are cultivated for ornamental flowers.

**EPIPHYTE**, the term used in botany to denote those plants which grow perched upon others. Epiphytes are a characteristic feature of tropical forests. Plants of many families have become adapted to this mode of life, notably orchids (*q.v.*). A feature of epiphytes is the development of aerial roots. (See *Root*.)

**ERICACEAE**, in botany, a family of plants belonging to the higher or sympetalous division of dicotyledons. They are mostly woody plants, with a slender creeping stem as in bilberry (blueberry), *Vaccinium* (fig. 1), or forming low bushes as in the heaths, or sometimes becoming tree-like, as in species of *Rhododendron*. The leaves are alternate, opposite or whorled in arrangement, and in form and structure show well-marked adaptation to life in dry or exposed situations. Thus in the true heaths they are needle-like, with the margins often rolled back to form a groove or an almost closed chamber on the under side. In others such as *Rhododendron* they are often leathery and evergreen, the strongly cuticularized upper surface protecting a water-storing tissue situated above the green layers of the leaf. The flowers are sometimes solitary and axillary or terminal as in *Andromeda*, but are generally arranged in racemose inflorescences at the end of the branches as in *Rhododendron*, or on small lateral shoots as in *Erica*. They are hermaphrodite and generally regular with parts in 4's or 5's, thus: sepals 4 or 5, petals 4 or 5, stamens 8 or 10 in two series, the

outer opposite the petals, and carpels 4 or 5. The corolla is usually more or less bell-shaped, and in the heaths persists in a dry state in the fruit. The petals with the stamens are situated on the outer edge of a honey-secreting disk. The anthers show great variety in shape, the halves being often more or less free and often appendaged; they open to allow the escape of the pollen by



AFTER DR. JOHN FLEMING'S DRAWING, BY COURTESY OF THE TRUSTEES OF THE BRITISH MUSEUM

FIG. 2.—RHODODENDRON (RHODODENDRON ARBOREUM)

a terminal pore or slit. The carpels are united to form a 4- or 5-chambered ovary, which bears a simple elongated style ending in a capitate stigma; each ovary chamber contains one to many ovules attached to a central placenta. The brightly coloured corolla, the presence of nectar and the scent render the flowers attractive to insects, and the projection of the stigma beyond the anthers favours crossing. The fruit is generally a capsule containing many seeds, as in *Erica* or *Rhododendron* (fig. 2); sometimes a berry, as in *Arbutus*.

The family falls into four distinct tribes, characterized by the relative position of the ovary and by the fruit and seed. They are:—

1. *Rhododendroideae*, characterized by capsular fruit, seed with a loose coat, deciduous petals and anthers without appendages. It consists mainly of the large genus *Rhododendron* (in which *Azalea* is included), which is chiefly developed in the mountains of eastern Asia, many species occurring on the Himalayas. *Dabeocia*, St. Dabeoc's heath, occurs in Ireland. In eastern America, *Kalmia* (laurel) is the prominent genus after *Rhododendron*.

2. *Arbutoideae*.—Fruit a berry or capsule, petals deciduous and anthers with bristle-like appendages, chiefly north temperate to Arctic in distribution. *Arbutus Unedo*, the strawberry-tree, so-called from its large scarlet berry, is southern European extending into south Ireland. *Arctostaphylos* (bearberry) and *Andromeda* are Arctic and alpine genera occurring in Britain and also extending from the Arctic into the mountainous regions of northern United States. *Epigaea repens* is the trailing arbutus or mayflower of Atlantic America.

3. *Vaccinioideae*.—Ovary inferior, fruit a berry. Extends from the north temperate zone to the mountains of the tropics. *Vaccinium*, the largest genus, has three British species: *V. Myrtillus* is the bilberry (*q.v.*), blueberry or whortleberry, *V. Vitis-Idaea* the cowberry, and *V. Oxycoccus* the cranberry (*q.v.*). There are 20 species recognized in the United States.

4. *Ericoideae*.—Fruit usually a capsule, seeds round, not winged; corolla persisting round the ripe fruit; anthers often appendaged. The largest genus is *Erica*, the true heath (*q.v.*), with 500 species, the majority confined to the Cape; others occur



FIG. 1.—BILBERRY (VACCINIUM MYRTILLUS), CLOSELY ALLIED TO THE HUCKLEBERRY AND VERY COMMON IN BRITAIN



on the mountains of tropical Africa and in Europe and north Africa, especially the Mediterranean region. *E. cinerea* (purple heather) and *E. Tetralix* (cross-leaved heath) are common British heaths. *Calluna* is the ling or Scotch heather. The genus is not represented in the United States.

**EUPHORBIACEAE**, in botany, a large family of flowering plants, containing 220 genera with about 4,000 species, chiefly tropical, but spreading over the whole earth with the exception of the Arctic and cold alpine zones. They are represented in Great Britain and North America chiefly by the spurges (*Euphorbia*, *q.v.*) (fig. 1), which are herbaceous, but the greater number are woody, often trees. The large genus *Euphorbia* shows great variety in habit; many species, like the English and most North American spurges, are annual herbs, others form bushes, while in the desert regions of tropical Africa and the Canary Islands species occur

resembling cacti, having thick fleshy stems and leaves reduced to spines. Another large genus, *Phyllanthus*, contains small annual herbs as well as trees, while in some species the leaves are reduced to scales, and the branches are flattened, forming phylloclades. The leaves also show great variety in form and arrangement, being simple and entire as in the English spurges, or deeply cut as seen in *Ricinus* (castor-oil) and *Manihot* or palmately compound (*Hevea*). The majority contain a milky juice or latex in their tissues which exudes on cutting or bruising. In *Hevea*, *Manihot* and others the latex yields caoutchouc. The flowers are unisexual; male and female flowers are borne on the same, as occurs in the spurges, or on different plants, as in dog's mercury. Their arrangement shows considerable variation, but the flowers are generally grouped in crowded definite partial inflorescences, which are themselves arranged in spikes or stand in the axils of the upper leaves. These partial inflorescences are generally unisexual, the male often containing numerous flowers while the female flowers are solitary. The partial inflorescence (*Cyathium*) of *Euphorbia* (fig. 1) resembles superficially a hermaphrodite flower. It contains a central terminal flower, consisting of a naked pistil; below this are borne four or five bracts which unite to form a cup-shaped involucre resembling a calyx; each of these bracts subtends a small cyme of male flowers each consisting only of one stamen. Between the segments of the cup are large oval or crescent-shaped glands, often brightly coloured, forming petal-like structures.

The form of the flower shows great variety. The most complete type occurs in *Wielandia*, a shrub from the Seychelles Islands, in which the flowers have their parts in fives, a calyx and corolla being succeeded in the male flower by 5 stamens, in the female by 5 carpels. Generally, however, only 3 carpels are present, as in *Euphorbia*; *Mercurialis* has minute apetalous flowers with 3 sepals, followed in the male by 8 to 20 stamens, in the female by a bicarpellary pistil. In many genera the corolla is absent. The most reduced type of flower is that described under EUPHORBIA. The stamens are sometimes more or less united (monadelphous), and in castor-oil (*Ricinus*) are much branched. The ovary generally contains three chambers, and bears three simple or more often bipartite styles; each chamber contains one or two pendulous ovules, which generally bear a cap-like outgrowth or *caruncle*, which persists in the seed.

As the stamens and pistil are borne by different flowers, cross-pollination is necessary. In *Mercurialis* and others with incon-



FIG. 1.—A SPURGE, EUPHORBIA HELIOSCOPIA, SHOWING GENERAL HABIT OF GROWTH

The cells of the plant contain latex, a milky-looking fluid

spicuous flowers pollination is effected by the wind, but in many cases insects are attracted to the flower by the highly-coloured bracts, as in many *Euphorbias* and *Dalechampia*, or by the coloured calyx as in *Manihot*; the presence of honey is also frequently an attraction, as in the honey-glands on the bracts of the cyathium of *Euphorbia*. The fruit is generally a capsule which splits into three divisions (*cocci*), separating from the central column, and splitting lengthwise into two halves. In the manchineel (*Hippomane Mancinella*) of Central America the fruit is a drupe like a plum, and in some genera berries occur. In the sandbox tree (*Hura crepitans*) of tropical America the ovary consists of numerous carpels, and forms when mature a capsule which splits with explosive violence into a number of woody cocci. The seeds contain abundant endosperm and a large embryo.

Several members of the family are of economic importance. *Manihot utilisima*, manioc or cassava (*q.v.*), is one of the most important tropical food-plants, its thick tuberous root being rich in starch; it is the source of Brazilian arrowroot. Caoutchouc or india-rubber is obtained from species of *Hevea*, *Mabea*, *Manihot* and *Sapium*. Castor-oil (*q.v.*) is obtained from the seeds of *Ricinus communis*. The seeds of *Aleurites tuloba* and *Sapium sebiferum* also yield oil. Resin is obtained from species of *Croton* and *Euphorbia*. Many of the species are poisonous; e.g., the South African *Toxicodendron*, one of the most poisonous plants known. Many, such as *Euphorbia*, *Mercurialis*, *Croton*, *Jatropha*, *Tragia*, have been, or still are, used as medicines. Species of *Codiaeum* (*q.v.*), *Croton*, *Euphorbia*, *Phyllanthus*, *Jatropha* and others are used as ornamental plants in gardens.

The box (*Buxus*) and a few allied genera, formerly included in Euphorbiaceae, are now generally regarded as forming a distinct family, Buxaceae, differing from Euphorbiaceae in the position of the ovule in the ovary-chamber and in the manner of splitting of the fruit.

**FAGACEAE**, in botany, the beech family; dicotyledonous plants, most of the 350 species being trees. The family includes five genera, the most important being *Fagus* (beech, *q.v.*), *Quercus* (oak, *q.v.*) and *Castanea* (chestnut, *q.v.*). The flowers are borne in catkins in the axils of the leaves, and are unisexual. The pollen is wind-borne. The fruit is a one-seeded nut.

**FLOWERLESS PLANTS:** see PTERIDOPHYTA, BRYOPHYTA, ALGAE, FUNGI.

**FOSSIL PLANTS:** see PALAEOBOTANY.

**FRANKENIACEAE**, in botany, the sea-heath family, comprising four genera and 60 species of salt-loving herbs, with jointed stems. There is one British species, *Frankenia laevis*, the sea-heath; and in North America, there are three species, *F. Jamesii*, found from Colorado to Texas; and *F. grandifolia*, the alkali-heath, and *F. Palmeri*, the *yerba reuma* of the Spanish Californians, both native to California.

**GENTIANACEAE** (the gentian family), in botany, a family of Dicotyledons belonging to the sub-class Sympetalae, and containing about 800 species and 80 genera. It has a world-wide distribution, and representatives adapted to very various conditions, including, for instance, alpine plants, like the true gentians (*Gentiana*), meadow plants such as the British *Chlora perfoliata* (yellow-wort) or *Erythraea Centaurium* (centaury), marsh plants such as *Menyanthes trifoliata* (bog-bean), floating water plants such as *Limnanthemum*, or steppe and sea-coast plants such as *Cicendia*. They are annual or perennial herbs, rarely shrubs, and generally growing erect, with a characteristic forked manner of branching; the Asiatic genus *Crawfurdia* has a climbing stem; they are often low-growing and caespitose, as in the alpine gentians.

The leaves are in decussating pairs (that is, each pair is in a plane at right angles to the previous or succeeding pair), except in *Menyanthes* and a few allied aquatic or marsh genera, where they are alternate or radical. Several genera, chiefly American, are saprophytes, forming slender low-growing herbs, containing little or no chlorophyll and with leaves reduced to scales; such is *Voyria*, mainly tropical American. The inflorescence is generally cymose, often dichasial, recalling that of Caryophyllaceae, the lateral branches often becoming monochasial; it is sometimes



reduced to a few flowers or one only, as in some gentians. The flowers are hermaphrodite and regular, with parts in fives and fives, with reproduction to two in the pistil; in *Chlora* there are six to eight members in each whorl. The calyx generally forms a tube with teeth or segments which usually overlap in the bud. The corolla shows great variety in form; thus among the British genera it is rotate in *Chlora*, funnel-shaped in *Erythraea*, and cylindrical, bell-shaped, funnel-shaped or salver-shaped in *Gentiana*; the segments are generally twisted to the right in the bud; the throat is often fimbriate or bears scales. The stamens, as many as, and alternating with, the corolla-segments, are inserted at very different heights on the corolla-tube; the filaments are slender, the anthers are usually attached dorsally, are versatile, and dehisce by two longitudinal slits; after escape of the pollen they sometimes become spirally twisted as in *Erythraea*. Dimorphic flowers are frequent, as in the bog-bean (*Menyanthes*). There is considerable variation in the size, shape and external markings of the pollen grains. The form of the honey-secreting developments of the disk at the base of the ovary also shows considerable variety. The superior ovary is generally one-chambered, with two variously developed parietal placentas, which occasionally meet, forming two chambers; the ovules are generally numerous and anatropous or half-anatropous in form. The style, which varies much in length, is simple, with an undivided or bilobed or bipartite stigma. The fruit is generally a membranous or leathery capsule, splitting septically into two valves; the seeds are small and numerous, and contain a small embryo in a copious endosperm.

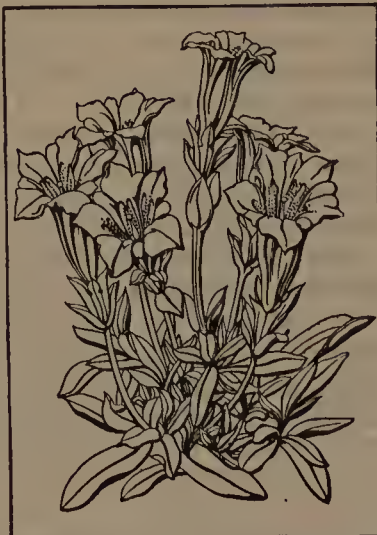
The brilliant colour of the flowers, which often occur in large numbers (as in the alpine gentians), the presence of honey-glands and the frequency of dimorphy and dichogamy, are adaptations for pollination by insect visitors. In the true gentians (*Gentiana*) the flowers of different species are adapted for widely differing types of insect visitors. Thus *Gentiana lutea*, with a rotate yellow corolla and freely exposed honey, is adapted to short-tongued insect visitors; *G. Pneumonanthe*, with a long-tubed, bright blue corolla, is visited by humble bees; and *G. verna*, with a still longer narrower tube, is visited by Lepidoptera.

*Gentiana*, the largest genus, contains about 400 species, distributed over Europe (including Arctic), five being British, the mountains of Asia, south-east Australia and New Zealand, the whole of North America (30 species) and along the Andes to Cape Horn; it does not occur in Africa. Bitter principles are general in the vegetative parts, especially in the rhizomes and roots, and have given a medicinal value to many species, e.g., *Gentiana lutea* and others. The next largest genus in North America is *Sabbatia* which has representatives from the Atlantic coast westward into the prairie region. (See GENTIAN.)

**GERANIACEAE**, in botany, a small but widely distributed family of Dicotyledons belonging to the Archichlamydeae, containing about 650 species in 11 genera. It is represented in Britain by two genera, *Geranium* (crane's-bill) and *Erodium* (stork's-bill), to which belong nearly two-thirds of the total number of species. The same two genera are the only representatives of the family in North America. The plants are mostly herbs, rarely shrubs, with generally simple glandular hairs on the stem and leaves. The opposite or alternate leaves have a pair of small stipules at the base of the stalk and a palminerved blade. The flowers, generally in a cymose inflorescence, are hermaphrodite, hypogynous, and, except in *Pelargonium*, regular. The parts are arranged in fives. There are five free sepals, overlapping in the bud, and, alternating with these, five free petals.

In *Pelargonium* the flower is zygomorphic with a spurred posterior sepal and the petals differing in size or shape. In *Geranium* the stamens are obdiplostemonous, i.e., an outer whorl of five opposite the petals alternates with an inner whorl of five opposite the sepals; at the base of each of the antisepalous stamens is a honey-gland. In *Erodium* the members of the outer whorl are reduced to scale-like structures (staminodes), and in *Pelargonium* from two to seven only are fertile. There is no satisfactory explanation of this break in the regular alternation of successive whorls. There are five, or fewer, carpels, which unite to form an ovary with as many chambers, in each of which are one or two, rarely more, pendulous anatropous ovules, attached to the central column in such a way that the micropyle points outwards and the raphe is turned towards the placenta. The long beak-like style divides at the top into a corresponding number of slender stigmas.

The larger-flowered species of *Geranium* are markedly protandrous, the outer stamens, inner stamens and stigmas becoming functional in succession. For instance, in meadow crane's-bill, *G. pratense*, each whorl of stamens ripens in turn, becoming



FROM REGEL, "GARTEN FLORA" (FERDINAND ENKE)

GENTIAN (*GENTIANA ACAULIS*), A STEMLESS ALPINE SPECIES



MEADOW CRANE'S-BILL (*GERANIUM PRATENSE*), AN ENGLISH HERB, WHOSE COMMON NAME IS DERIVED FROM ITS LONG-BEAKED FRUIT. THE DOUBLE-FLOWED VARIETIES ARE FREQUENTLY GROWN IN GARDEN BORDERS

erect and shedding their pollen; as the anthers wither the filaments bend outwards, and when all the anthers have diverged the stigmas become mature and ready for pollination. By this arrangement self-pollination is prevented and cross-pollination ensured by the visits of bees which come for the honey secreted by the glands at the base of the inner stamens.

In species with smaller and less conspicuous flowers, such as *G. molle*, self-pollination is possible, since the divisions of the stigma begin to separate before the outer stamens have shed all their pollen; the nearness of the stigmas to the dehiscing anthers favours self-pollination.

In the ripe fruit the carpels separate into five one-seeded portions (*cocci*), which break away from the central column,



either rolling elastically outwards and upwards or becoming spirally twisted. In most species of *Geranium* the cocci split open on the inside and the seeds are shot out by the elastic up-twisting (fig. 1); in *Erodium* and *Pelargonium* each coccus remains closed, and the long twisted upper portion separates from the central column, forming an awn, the distribution of which is favoured by the presence of bristles or hairs. The embryo generally fills the seed, and the cotyledons are rolled or folded on each other.

*Geranium* is the most widely distributed genus; it has 300 species and is spread over all temperate regions with a few species in the tropics. Three British species—*G. sylvaticum*, *G. pratense* and *G. Robertianum* (herb-Robert)—reach the Arctic zone, while *G. patagonicum* and *G. magellanicum* are found in the Antarctic. *Erodium* contains 65 species (two are British), most of which are confined to the Mediterranean region and west Asia, though others occur in America, in South Africa and West Australia. *Geranium* is represented in eastern United States by 11 species, 7 of which are introduced. In this region *Erodium* is represented only by two species introduced from Europe. In the western United States there are 5 species of *Geranium*, and *Erodium* is represented by one native species which extends throughout the whole region west of the Rocky Mountains, where it is known as "pin-clover" and "pin-grass." *Pelargonium*, with 250 species, has its centre in South Africa; the well-known garden and greenhouse "geraniums" are species of *Pelargonium* (see GERANIUM.)

**GERMINATION**, of seeds, see ANGIOSPERMS: *Germination of Seed*.

**GRAFT HYBRIDS**: see CHIMAERA.

**GRAMINEAE**, in botany, the grass family (see GRASSES), comprising about 450 genera and 4,500 species.

**HALOPHYTES**, a general name used in botany to denote plants growing in salt marshes and similar environments with a high salt content. Such plants show adaptations for conservation of water. (See PLANTS: *Ecology*.)

**HYDROCHARITACEAE**, in botany, a family of monocotyledons, belonging to the series Helobieae. They are water-

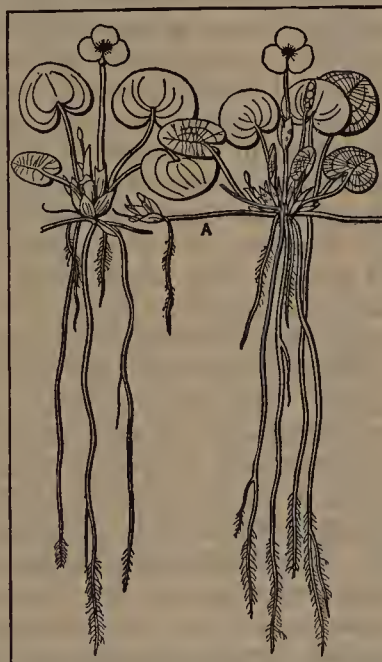
plants, represented in Britain by frog-bit (*Hydrocharis Morsusranae*) and water-soldier (*Stratiotes aloides*). The family contains about 50 species in 13 genera, 10 of which occur in fresh water while 3 are marine: and includes both floating and submerged forms. *Hydrocharis* floats on the surface of still water, and has rosettes of kidney-shaped leaves, from among which spring the flower-stalks; stolons bearing new leaf-rosettes are sent out on all sides, the plant thus propagating itself in the same way as the strawberry. *Stratiotes aloides* has a rosette of stiff, sword-like leaves, which project above the surface when the plant is in flower. It is stoloniferous, the young rosettes sinking to the bottom at the beginning of winter and rising again to the surface in the spring. *Vallisneria* (eel-grass)

contains two species, one native of tropical Asia, the other inhabiting the warmer parts of both hemispheres and reaching as far north as south Europe. It grows in the mud at the bottom of fresh water, and the short stem bears a cluster of long, narrow, grass-like leaves. New plants are formed at the end of horizontal runners. Another type is represented by *Elodea canadensis* or water-thyme, which has been introduced into the British Isles from North America. It is a small, submerged plant with long, slender, branching stems bearing whorls of narrow, toothed leaves; the flowers appear at the surface when mature. In *Hydrocharis*, a dioe-

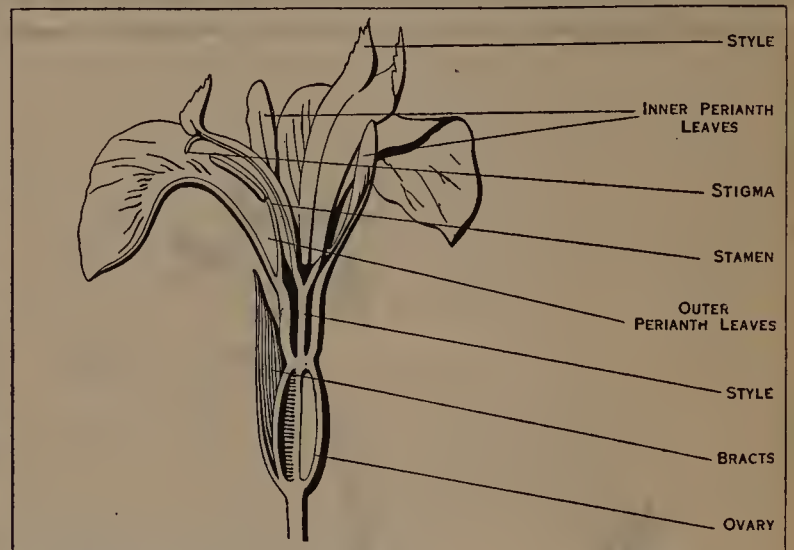
cious plant, the flowers are borne above the surface of the water, have conspicuous white petals, contain honey and are pollinated by insects. *Stratiotes* has similar flowers which come above the surface only for pollination, becoming submerged again during ripening of the fruit. In *Vallisneria* which is also dioecious, the small male flowers are borne in large numbers in short-stalked spathes; the petals are minute and scale-like, and only two of the three stamens are fertile; the flowers become detached before opening and rise to the surface, where the sepals expand and form a float bearing the two projecting semi-erect stamens. The female flowers are solitary and are raised to the surface on a long, spiral stalk; the ovary bears three broad styles, on which some of the large, sticky pollen-grains from the floating male flowers get deposited. After pollination the female flower is drawn below the surface by the spiral contraction of the long stalk, and the fruit ripens near the bottom.

The family is a widely distributed one; the marine forms are tropical or subtropical, but the fresh-water genera occur also in the temperate zones. In addition to the water-thyme (*Elodea*), found across the continent, and the eel-grass (*Vallisneria*), of the eastern States and Canada, the family is represented in North America by the American frog-bit (*Limnobium Spongia*), of the southeastern States, and the marine *Halophila Engelmannii*, of the Florida coast.

**IRIDACEAE** (the iris family), in botany, a family of flowering plants belonging to the order Liliiflorae of the class Monocotyledons, containing about 800 species in 60 genera, and widely distributed in temperate and tropical regions. The members of this family are generally perennial herbs growing from a corm as



FROG-BIT (*HYDROCHARIS MORSUS-RANAE*), COMMON IN EUROPE AND THE GREATER PART OF ASIA



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL)

IRIS (*IRIS PSEUDACORUS*). LONGITUDINAL SECTION THROUGH FLOWER

*Crocus* and *Gladiolus*, or a rhizome as *Iris*; more rarely, as the Spanish iris, from a bulb. A few South African representatives have a shrubby habit. The flowers are hermaphrodite and regular as in *Iris* and *Crocus*, or with a symmetry in the median plane as in *Gladiolus*. The arrangement of the flower parts resembles that in the nearly allied order Amaryllidaceae (*Narcissus*, *Snowdrop*), but differs in the absence of the inner whorl of stamens.

The most important genera are *Crocus* (q.v.), with about 60 species, *Iris* (q.v.), with about 200 and *Gladiolus* (q.v.), with 150. *Ixia*, *Freesia* (q.v.) and *Tritonia* (including *Montbretia*), all natives of South Africa, are well known in cultivation. *Sisyrinchium*, blue-eyed grass, is a new-world genus of 75 species, extending from arctic America to Patagonia and the Falkland Isles. One species, *S. angustifolium*, an Arctic and temperate North American species, is also native in Galway and Kerry in Ireland. Other British representatives of the family are: *Iris Pseudacorus* (yellow iris), common by river-banks and ditches, *I. foetidissima* (stinking iris), *Gladiolus illyricus*, a rare plant found in the New Forest and the Isle of Wight, and *Romulea Columnae*, a small plant with narrow recurved leaves a few inches long and a short scape bearing one or more small regular funnel-



shaped flowers, which occurs at Dawlish in Devonshire. In the eastern United States there are 10 species of *Iris* and 13 species of *Sisyrinchium*, but in the Rocky Mountain region these genera are represented by only 2 or 3 species.

**JUNCACEAE** (rush family), in botany, a family of flowering plants belonging to the series Liliiflorae of the class Monocotyledones, containing about 800 species in seven genera, widely distributed in temperate and cold regions. It is represented in Great Britain by the two out of the eight genera which comprise the whole family—*Juncus*, rush, and *Luzula*, wood-rush. The same two genera represent the family throughout North America. They are generally perennial herbs with a creeping underground stem and erect, unbranched, aerial stems, bearing slender leaves which are grass-like or cylindrical or reduced to membranous sheaths. The small inconspicuous flowers are generally more or less crowded in terminal or lateral clusters, the form of the inflorescence varying widely according to the manner of branching and the length of the pedicels. The flowers are hermaphrodite and regular, with the



IRIS



GREAT HAIRY WOOD-RUSH

same number and arrangement of parts as in the family Liliaceae, from which they differ in the inconspicuous membranous character of the perianth, the absence of honey or smell, and the brushlike stigmas with long papillae—adaptations to wind-pollination as

contrasted with the methods of pollination by insect agency, which characterize the Liliaceae. Juncaceae are, in fact, a less elaborated group of the same series as Liliaceae, but adapted to a simpler and more uniform environment than that larger and much more highly developed family.

**LABIATAE**, in botany, a family of seed-plants belonging to the series of Tubiflorae of the dicotyledons, and containing about 200 genera with 3,000 species. The majority are annual or perennial herbs inhabiting the temperate zone, becoming shrubby in warmer climates. The stem is generally square in section and the simple exstipulate leaves are arranged in decussating pairs (*i.e.*, each pair is in a plane at right angles to that of the pairs immediately above and below it); the blade is entire, or toothed, lobed or more or less deeply cut. The plant is often hairy, and the hairs are frequently glandular, the secretion containing a scent characteristic of the genus or species. The flowers are borne in the axils of the leaves or bracts; they are rarely solitary as in *Scutellaria* (skull-cap), and generally form an apparent whorl (*verticillaster*) at the node, consisting of a pair of cymose inflorescences each of which is a simple three-flowered dichasium as in *Brunella*, *Salvia*, etc., or more generally a dichasium passing over into a pair of monochasial cymes as in *Lamium*, *Ballota*, and *Nepeta*. A number of whorls may be crowded at the apex of the stem and the subtending leaves reduced to small bracts, the whole forming a raceme- or spike-like inflorescence as in *Mentha*, *Brunella*, etc. The plan of the flower is remarkably uniform; it is bisexual and zygomorphic in the median plane, with 5 sepals united to form a persistent cup-like calyx, 5 petals united to form a two-lipped gaping corolla, 4 stamens inserted on the corolla-tube, two of which, generally the anterior pair, are longer than the other two (didynamous arrangement)—sometimes as in *Salvia*, the posterior pair is aborted—and two superior median carpels, each very early divided by a constriction in a vertical plane, the pistil consisting of four cells each containing one erect anatropous ovule attached to the base of an axile placenta; the style springs from the centre of the pistil between the four segments (*gynobasic*), and is simple with a bifid apex. The fruit comprises four one-seeded nutlets included in the persistent calyx; the seed has a thin testa and the embryo almost or completely fills it. Although the general form and plan of arrangement of the flower is very uniform, there are wide variations in detail. Thus the calyx may be tubular, bell-shaped, or almost spherical, or straight or bent, and the length and form of the teeth or lobes varies also; it may be equally toothed as in mint (*Mentha*) and marjoram (*Origanum*), or two-lipped as in thyme (*Thymus*), *Lamium*, *Monarda* and *Salvia*; the number of nerves affords useful characters for distinction of genera; there are normally five main nerves between which simple or forked secondary nerves are more or less developed. The shape of the corolla varies widely, the differences being doubtless intimately associated with the pollination of the flowers by insect agency. The tube is straight or variously bent and often widens towards the mouth. Occasionally the limb is equally five-toothed, or forms, as in *Mentha* an almost regular four-toothed corolla by union of the two posterior teeth. Usually it is two-lipped with an upper lip and lower lip; the median lobe of the lower lip is generally most developed and forms a resting-place for the bee or other insect when probing the flower for honey. The upper lip shows great variety in form, often, as in *Lamium* and *Stachys*, it is arched, forming a protection from rain for the stamens, or it may be flat as in thyme. In the tribe *Ocimoideae* the four upper petals form the upper lip; and the single anterior one the lower lip, and in *Teucrium* the upper lip is absent, all five lobes being pushed forward to form the lower. The posterior stamen is sometimes present as a staminode, but generally suppressed; the upper pair are often reduced to staminodes or more or less completely suppressed as in *Salvia*, rarely are these developed and the anterior pair reduced. In *Nepeta* and allied genera the posterior pair are the longer, but this is rare, the didynamous character being generally the result of the anterior pair being the longer. The anthers are two-celled, each cell splitting lengthwise; the connective may be more or less developed between the cells. An extreme case is seen in *Salvia*, where the connective is filiform and jointed to the



filament, while the anterior anther-cell is reduced to a sterile appendage. Honey is secreted by a hypogynous disk. In the more general type of flower the anthers and stigmas are protected by the arching upper lip as in dead-nettle and many other British genera; the lower lip affords a resting-place for the insect which in probing the flower for the honey, secreted on the lower side of the disk, collects pollen on its back. Numerous variations in detail are found in the different genera; in *Salvia*, for instance, there is a lever mechanism, the barren half of each anther forming a knob at the end of a short arm which when touched by the head of an insect causes the anther at the end of the longer arm to descend on



WHITE DEAD-NETTLE (*LAMIAM ALBUM*), SHOWING TYPICAL HABIT OF GROWTH AND THE SQUARE HAIRY STEM. CROSS-POLLINATION IS ASSURED BY BEES VISITING THE FLOWERS

the insect's back (see POLLINATION). Brightly-coloured flowers with longer tubes adapted to the visits of butterflies and moths, as species of *Salvia*, *Stachys*, *Monarda*, are also found; some South American species of *Salvia* are pollinated by the humming-birds. In *Mentha*, thyme, marjoram (*Origanum*), and allied genera, the flowers are nearly regular and the stamens spread beyond the corolla.

The persistent calyx encloses the ripe nutlets, and aids in their distribution in various ways, by means of winged spiny or hairy lobes or teeth; sometimes it forms a swollen bladder. A scanty endosperm is sometimes present in the seed; the embryo is generally parallel to the fruit axis with a short inferior radicle and generally flat cotyledons.

The family occurs in all warm and temperate districts; its chief centre is the Mediterranean region, where some genera such as *Lavandula*, *Thymus*, *Rosmarinus* and others form an important feature in the vegetation. The tribe *Ocimoideae* is exclusively tropical and subtropical and occurs in both hemispheres. The family is well represented in Britain by nineteen native genera; *Mentha* (mint) including also *M. piperita* (peppermint) and *M. Pulegium* (pennyroyal); *Origanum vulgare* (marjoram); *Thymus*

*Serpyllum* (thyme); *Calamintha* (calamint), including also *C. Clinopodium* (wild basil) and *C. Acinos* (basil thyme); *Salvia* (sage), including *S. pratensis* (clary); *Nepeta Cataria* (catmint); *N. Glechoma* (ground-ivy); *Brunella* (self-heal); *Scutellaria* (skull-cap); *Stachys* (woundwort); *S. Betonica* (wood betony); *Galeopsis* (hemp-nettle); *Lamium* (dead-nettle); *Ballota* (black horehound); *Teucrium* (germander); and *Ajuga* (bugle).

Labiatae are readily distinguished from all other families of the series excepting Verbenaceae, in which, however, the style is terminal; but several genera, e.g., *Ajuga*, *Teucrium* and *Rosmarinus*, approach Verbenaceae in this respect, and in some genera of that order the style is more or less sunk between the ovary lobes. The fruit-character indicates an affinity with Boraginaceae from which, however, they differ in habit and by characters of ovule and embryo.

The presence of volatile oil renders many genera of economic use, such as thyme, marjoram (*Origanum*), sage (*Salvia*), lavender (*Lavandula*), rosemary (*Rosmarinus*), patchouli (*Pogostemon*). The tubers of *Stachys Sieboldi* are eaten in France.

The family is represented in North America by about 40 genera the largest being *Teucrium* (germander), *Scutellaria* (skull-cap), *Marrubium* (horehound), *Nepeta* (catnip), *Physostegia* (dragon-head), *Leonurus* (motherwort), *Stachys* (hedge nettle), *Salvia* (sage), *Monarda* (horsemint), *Hedeoma* (pennyroyal), *Thymus* (Thyme), and *Mentha* (mint).

**LAURACEAE**, a family of dicotyledonous trees and shrubs, the best-known members of which are the laurels (*q.v.*). There are 40 genera and 1,000 species, nearly all tropical and subtropical and especially numerous in south-eastern Asia and in Brazil. The leaves are leathery and evergreen; the tissues contain oil-cavities; the flowers are without petals, the parts usually arranged in threes; the fruit is a berry. Besides the laurel (*Laurus*), the family includes the cinnamon, cassia and camphor (*Cinnamomum*), the avocado-pear (*Persea*) and numerous valuable medicinal plants. In North America the family is represented by several trees and shrubs, found chiefly in the southern United States, like the sassafras, spice-bush and Oregon myrtle (*qq.v.*).

**LINACEAE**, in botany, the flax family, comprising nine genera and 150 species, mostly herbs and shrubs. The only important genus of this family of dicotyledons is *Linum*. (See FLAX, LINSEED.)

**LORANTHACEAE**, in botany, the mistletoe family, containing 30 genera and 520 species. All the members of this dicotyledonous family are parasitic plants with green leaves. The only British species is *Viscum album*, the mistletoe (*q.v.*). In the United States the family is represented by about six species of *Phoradendron* (American mistletoe) and some eight species of *Arceuthobium* (pine mistletoe).

**MALVACEAE**, in botany a large and economically important family of flowering plants. It contains 45 genera with about 900 species, and occurs in all regions except the coldest, the number of species increasing as we approach the tropics. The most conspicuously useful plant is cotton (*Gossypium*). It is represented in Britain by three genera: *Malva*, mallow; *Althaea*, marsh-mallow; and *Lavatera*, tree-mallow. In the United States there are about 20 genera, the best known ones, after *Gossypium*, being *Althaea* (marsh-mallow and hollyhock), *Malva* (mallow), *Sida Abutilon* (Indian mallow or velvet-leaf), and *Hibiscus* (rose mallow, and also okra or gumbo). The plants are herbs, as in the British mallows, or, in the warmer parts of the earth, shrubs or trees. The leaves are alternate and often palmately lobed or divided; the stipules generally fall early. The leaves and young shoots often bear stellate hairs and the tissues contain mucilage-sacs. The regular, hermaphrodite, often showy flowers are borne in the leaf-axils, solitary or in fascicles, or form more or less complicated cymose arrangements. An epicalyx formed by a whorl of three or more bracteoles is generally present just beneath the calyx; sometimes, as in *Abutilon*, it is absent. The parts of the flowers are typically in fives; the five sepals, which have a valvate aestivation, are succeeded by five often large showy petals which are twisted in the bud; they are free to the base, where they are attached to the staminal tube and fall with it when the flower



withers. The very numerous stamens are united into a tube at the base, and bear kidney-shaped one-celled anthers which open by a slit across the top. The large spherical pollen-grains are covered with spines. The carpels are one to numerous; when five in number, as in *Abutilon*, they are opposite the petals, or, as in *Hibiscus*, opposite the sepals. In the British genera and many others they are numerous, forming a whorl around the top of the axis in the



HIBISCUS (*HIBISCUS ESCULENTUS*), SHOWING UPPER PART OF FLOWERING PLANT (ANNUAL) AND AN UNRIPE FRUIT

centre of the flower, the united styles rising from the centre and bearing a corresponding number of stigmatic branches. In *Malope* the numerous carpels are arranged one above the other in vertical rows. One or more anatropous ovules are attached to the inner angle of each carpel; they are generally ascending but sometimes pendulous or horizontal; the position may vary, as in *Abutilon*, in one and the same carpel.

The flowers are protandrous; when the flower opens the unripe stigmas are hidden in the staminal tube and the anthers occupy the centre of the flower; as the anthers dehisce the filaments bend backwards and finally the ripe stigmas spread in the centre. Pollination is effected by insects which visit the flower for the honey, which is secreted in pits one between the base of each petal and is protected from rain by hairs on the lower margin of the petals. In small pale-flowered forms, like *Malva rotundifolia*, which attract few insects, self-pollination is found, the style-arms twisting later to bring the stigmatic surfaces into contact with the anthers.

Except in *Malva viscus* which has a berry, the fruits are dry. In *Malva* (see MALLOW) and allied genera they form one-seeded schizocarps separating from the persistent central column and from each other. In *Hibiscus* and *Gossypium* (the cotton-plant), the fruit is a capsule splitting loculicidally. Distribution of the seeds is sometimes aided by hooked outgrowths on the wall of the schizocarp, or by a hairy covering on the seed, an extreme case of which is the cotton-plant where the seed is buried in a mass of long tangled hairs—the cotton. The embryo is generally large with much-folded cotyledons and little endosperm.

The largest genus, *Hibiscus*, contains 160 species, which are widely distributed chiefly in the tropics; *H. Rosa sinensis* is a well-known greenhouse plant. *Abutilon* (*q.v.*) contains 120 species, mainly tropical; *Lavatera*, with 20 species, is chiefly Mediterranean; *Althaea* has about 15 species in temperate and warm regions, *A. rosea* being the hollyhock (*q.v.*); *Malva* has about 30 species in the north-temperate zone. Several genera are largely or exclusively American.

**MARANTACEAE**, in botany the arrowroot family, monocotyledonous perennials, comprising 27 genera and 300 species, all tropical and mainly American. The West Indian *Maranta arundinacea* is the source of arrowroot (*q.v.*).

**MELASTOMACEAE**, a large family of dicotyledonous plants, comprising 200 genera and 2,500 species, nearly all tropical and sub-tropical. The family is represented in the eastern and southern United States by about 10 species of *Rhexia* (meadow-beauty). A few yield dyes and many are cultivated for their ornamental flowers. Some species live in harmony with ants, the ants finding shelter within the plant, which is thus protected from the ravages of the leaf-cutter ants. (See MEADOW-BEAUTY.)

**MONOCOTYLEDONS:** see ANGIOSPERMS.

**MORACEAE**, in botany, a family of dicotyledons, belonging to the series *Urticales*, to which belongs also the nettle family



BY COURTESY OF THE ROYAL HORTICULTURAL SOCIETY

BLACK MULBERRY (*MORUS NIGRA*), SHOWING BRANCH WITH FRUIT

(*Urticaceae, q.v.*). It contains about 55 genera with about 800 species, mostly trees or shrubs, widely distributed in the warmer parts of the earth. The largest genus, *Ficus* (the fig, *q.v.*), contains 800 species spread through tropical and sub-tropical regions, and includes the common fig of the Mediterranean region (*Ficus carica*), the banyan (*F. benghalensis*), and the india-rubber plant (*F. elastica*); many of the species are epiphytic, sometimes clinging so tightly round the host-plant with their roots as to strangle it. *Morus* (mulberry, *q.v.*) contains ten species of trees or bushes in north temperate regions and in the mountains of the tropics. *Artocarpus*, including *A. incisa* (bread-fruit, *q.v.*), and *A. integrifolia* (jack-tree), has forty species, chiefly natives of the Indian Archipelago. The plants are rich in latex which may be very poisonous, as in *Antiaris toxicaria*, the Upas tree (*q.v.*) of Java, or sweet and nutritious as in *Brosimum Galactodendron*, the cow-tree (*q.v.*) of Venezuela. The latex often yields caoutchouc as in species of *Ficus* (e.g., *F. elastica*), *Cecropia* (*q.v.*), a tropical American genus with thirty to forty species, and others. In eastern United States the family is represented by *Morus* (mulberry) and one species of *Maclura* (osage orange), the latter being much planted for hedges. In the western United States (Rocky Mountain region) there are no native representatives of the family.

From the evidence of leaf-fossils, it is probable that the genus *Ficus* existed as far north as Greenland in the Cretaceous era and was generally distributed in North America and Europe in the Tertiary period up to Miocene times.

**MUSACEAE**, in botany, the banana family, monocotyledonous plants divided into six genera and about 70 species, all



tropical and mostly gigantic herbs. *Ravenala madagascariensis* is called the traveller's tree, as water accumulates in the leaf-bases and can be used for drinking. *Musa* includes the banana and plantain and also Manila hemp (*qq.v.*).

**MYCOLOGY** is the science of fungi (Greek *μύκης*, a mushroom, *λόγος*, discourse), and is dealt with in the article FUNGI.

**MYRISTICACEAE**, in botany, the nutmeg family, comprising 18 genera and 275 species, all tropical and especially numerous in Asia. They are trees or shrubs with evergreen leaves. (See NUTMEG.)

**MYRTACEAE**, in botany, the myrtle or eucalyptus family, dicotyledonous trees and shrubs found in all the warmer parts of the world, especially in Australia and tropical America. There are about 90 genera and some 2,800 species, all with oil-glands in the evergreen leaves. Several species yield useful timber, and *Eucalyptus* also gives oil; *Eugenia*, cloves, etc. Some have edible fruits, as *Pisidium* (guava), *Rhodomyrtus* (hill-gooseberry) and *Feijoa* (pineapple guava). *Pimenta officinalis* yields allspice (*q.v.*) and *P. acris*, bay oil. (See EUCALYPTUS; FEIJOA; GUAVA.)

**OLEACEAE**, in botany, the olive family, dicotyledonous shrubs and trees of warm, temperate and tropical regions, especially abundant in the East Indies. *Fraxinus* includes the ash (*q.v.*) and flowering ash (*F. Ormus*). *Olea* includes the olive (*q.v.*) and the black ironwood tree (*O. laurifolia*). The family includes also numerous valuable ornamental trees and shrubs, as privet, jasmine, lilac, golden-bells, and fringe-tree. There are 21 genera and about 500 species, some 40 of which occur in North America.

**ONAGRACEAE**, in botany, a family of dicotyledons belonging to the order Myrtiflorae, to which belongs also the myrtle family, Myrtaceae. It contains about 40 genera and 500 species, and occurs chiefly in the temperate zone of the New World, especially on the Pacific side. It is represented in Britain by several species of *Epilobium* (willow-herb), *Circaea* (enchanter's nightshade), and *Ludvigia*, a small perennial herb very rare in boggy pools in Sussex and Hampshire. In the United States, especially in the Pacific States, the family is well represented, the principal genera being *Oenothera* (containing as a native the evening primrose, now naturalized in certain parts of Europe), *Epilobium* (willow herb), and *Ludvigia* (false loosestrife). The plants are generally herbaceous, sometimes annual, as species of *Epilobium*, *Clarkia*, *Godetia*, or biennial, as *Oenothera biennis*—evening primrose—or sometimes become shrubby or arborescent, as *Fuchsia* (*q.v.*). The simple leaves are generally entire or inconspicuously toothed, and are alternate, opposite or whorled in arrangement; they are generally exstipulate. The flowers are often solitary in the leaf-axils, as in many *Fuchsias*, *Clarkia*, etc., or associated, as in *Epilobium* and *Oenothera*, in large showy terminal spikes or racemes; in *Circaea* the small white or red flowers are borne in terminal and lateral racemes. The regular flowers have the parts in fours, the typical arrangement as illustrated by *Epilobium*, *Oenothera* and *Fuchsia* being as follows: 4 sepals, 4 petals, two alternating whorls of 4 stamens, and 4 inferior carpels. The floral receptacle is produced above the ovary into the so-called calyx-tube, which is often petaloid, as in *Fuchsia*, and is sharply distinguished from the ovary, from which it separates after flowering.

In *Clarkia* the inner whorl of stamens is often barren, and in

*Eucharidium* it is absent. In *Circaea* the flower has its parts in two's. Both sepals and petals are free; the former are valvate in bud, and reflexed in the flower; in *Fuchsia* they are petaloid. The petals are generally convolute in bud; they are entire (*Fuchsia*) or bilobed (*Epilobium*); in some species of *Fuchsia* they are small and scale-like, or absent (*F. apetala*). The stamens are free, and those of the inner whorl are generally shorter than those of the outer whorl. The flowers of *Lopezia* (Central America) have only one fertile stamen. The large spherical pollen grains are connected by viscid threads. The typically quadrilocular ovary contains numerous ovules on axile placentas; the 1-to-2-celled ovary of *Circaea* has a single ovule in each loculus. The long slender style has a capitate (*Fuchsia*), 4-rayed (*Oenothera*, *Epilobium*) or 4-notched (*Circaea*) stigma. The flowers, which have generally an attractive corolla and honey secreted by a swollen disk at the base of the style or on the lower part of the "calyx-tube," are adapted for pollination by insects, chiefly bees and lepidoptera; sometimes by night-flying insects when the flowers are pale and open towards evening, as in evening primrose. The fruit is generally a capsule splitting into four valves and leaving a central column on which the seeds are borne as in *Epilobium* and *Oenothera*—in the former the seeds are scattered by aid of a long tuft of silky hairs on the broader end. In *Fuchsia* the fruit is a berry, which is sometimes edible, and in *Circaea* a nut bearing recurved bristles. The seeds are exalbuminous. Several of the genera are well known as garden plants, e.g., *Fuchsia*, *Oenothera*, *Clarkia* and *Godetia*. Evening primrose (*Oenothera biennis*), a native of North America, occurs apparently wild as a garden escape in Britain. *Jussieua*, a tropical genus of 50 species of water- and marsh-herbs, shows a development of well-developed aerating tissue.

**PINACEAE**: see GYMNASPERMS.

**PIPERACEAE**, in botany, the pepper family, comprising seven genera with 1,150 species, tropical herbs and shrubs. The leaves have a pungent flavour and the flowers lack both calyx and corolla. *Piper* includes the pepper (*q.v.*).

**PLANTAGINACEAE**, a family of dicotyledonous herbs, the best known members of which are the plantains (*Plantago*), cosmopolitan weeds, of which five species occur in Great Britain and upwards of 30 in the United States. (See PLANTAIN.) The family contains three genera and about 200 species. The seeds of *Plantago Psyllium* (Mediterranean) are used in silk and cotton manufacture. The flowers, usually hermaphrodite and inconspicuous, are wind-pollinated.

**PODOCARPACEAE**: see GYMNASPERMS.

**PODOSTEMACEAE**, a remarkable family of dicotyledonous plants, living only on rocks in rushing water. The seeds are shed on the rocks during the dry season, germinating when the rocks become submerged in the rainy season. The vegetative parts consist mainly of a flattened green thallus, usually derived from adventitious roots. There are 22 genera and about 100 species, nearly all tropical, a single representative, *Podostemon Ceratophyllum* (river-weed), occurring in North America, found in shallow streams from Massachusetts to Minnesota and southward to Georgia and Alabama. (See J. C. Willis, *Ann. Perad.* [1902].)

**POLYGALACEAE**, a family of dicotyledonous herbs, shrubs and small trees, comprising ten genera and about 700 species, not represented in New Zealand, Polynesia and the Arctic zone, but otherwise cosmopolitan. *Polygala vulgaris* is the British milkwort (*q.v.*), and *P. Senega*, the Senega snake-root, a North American medicinal plant. In North America some 50 species are found, chiefly in the southern and western United States.

**POLYGONACEAE**, in botany, a family of dicotyledons, containing 40 genera with about 750–800 species, chiefly in the north temperate zone, and represented in Great Britain by three genera, *Polygonum*, *Rumex* (dock, *q.v.*) and *Oxyria*. They are mostly herbs characterized by the union of the stipules into a sheath or *ocrea*, which protects the younger leaves in the bud stage. Some are climbers, as, for instance, the British *Polygonum Convolvulus* (black bindweed). In *Muehlenbeckia platyclada*, a native of the Solomon islands, the stem and branches are flattened,



GREAT HAIRY WILLOWHERB (EPILOBIUM HIRSUTUM)



forming ribbon-like cladodes jointed at the nodes. The leaves are alternate, simple and generally entire; the edges are rolled back in the bud. They are generally smooth, but sometimes, especially in mountain species, woolly. The small regular, generally hermaphrodite flowers are borne in large numbers in compound inflorescences, the branches of which are cymose. The parts of the flower are whorled (cyclic) or acyclic. The former arrangement may be derived from a regular trimerous flower with two whorls of perianth leaves, two staminal whorls and a three-sided ovary—this type of flower occurs in the Californian genus *Pterostegia*. The flower of rhubarb (*Rheum*) is derived from this by doubling in the outer staminal whorl and that of the dock (*Rumex*) by doubling in the outer staminal whorl and suppression of the inner whorl. Dimerous whorled flowers occur in *Oxyria* (mountain sorrel), another Arctic and alpine genus, the flowers of which otherwise resemble those of *Rumex*. In the acyclic flowers a pentamerous perianth is followed by five to eight stamens as in *Polygonum*. The perianth leaves are generally uniform and green, white or red in colour. They are free or more or less united, and persist till the fruit is ripe, often playing a part in its distribution, and affording useful characters for distinguishing genera or species. Thus in the docks the three inner leaves enlarge and envelop the fruit as three membranous wings one or more of which bear on the back large fleshy warts. The number of the carpels is indicated by the three-sided (in dimerous flowers two-sided) ovary, and the number of the styles; the ovary is unilocular and contains a single erect ovule springing from the top of the floral axis. The fruit is a dry one-seeded nut, two-sided in bicarpelary flowers, as in *Oxyria*. The straight or curved embryo is embedded in a mealy endosperm. The flowers are wind-pollinated, as in the docks (*Rumex*), where they are pendulous on long slender stalks and have large hairy stigmas; or insect-pollinated, as in *Polygonum* or rhubarb (*Rheum*), where the stigmas are capitate and honey is secreted by glands near the base of the stamens. Insect-pollinated flowers are rendered conspicuous chiefly by their aggregation in large numbers, as for instance in bistort (*Polygonum Bistorta*), where the perianth is red and the flowers are crowded in a spike. In buckwheat (*q.v.*, *P. Fagopyrum*) the numerous flowers have a white or red perianth and are perfumed; they are dimorphic, *i.e.*, there are two forms of flowers, one with long styles and short stamens, the other with short styles and long stamens. In other cases self-pollination is the rule, as in knot-grass (*P. aviculare*), where the very small, solitary odourless flowers are very rarely visited by insects and pollinate themselves by the incurving of the three inner stamens on to the styles.

Polygonaceae is mainly a north temperate order. A few genera are tropical, *e.g.*, *Coccoloba*, which has 125 species restricted to tropical and sub-tropical America. *Polygonum* has a very wide distribution spreading from the limits of vegetation in the northern hemisphere to the mountains of tropical Africa and South Africa, through the highlands of tropical Asia to Australia, and in America as far south as Chile. Most of the genera have, however, a limited distribution. In the British Isles, *Polygonum* has 14 species; *Rumex* (12 species) includes the various species of dock (*q.v.*) and sorrel (*R. Acetosa*); and *Oxyria digyna*, an alpine plant (mountain sorrel), takes its generic name (Gr. ὀξύς, sharp) from the acidity of its leaves. *Rheum* (rhubarb, *q.v.*) is central Asiatic.

In the United States the largest genus is *Eriogonum*, containing about 200 species, all natives of America, and most of them in the western United States. The other prominent genera occurring in America are *Rumex* (docks), *Persicaria* (smartweeds), and *Polygonum* (knotweeds). *Fagopyrum* (buckwheat) and *Rheum* (rhubarb or pie-plant) also are abundant, but they are natives of the Old World.

**PRIMULACEAE**, in botany, a family of gamopetalous dicotyledons belonging to the order Primulales and containing 25 genera with about 550 species. It is cosmopolitan in distribution, but the majority of the species are confined to the temperate and colder parts of the northern hemisphere and many are Arctic or alpine. Nine genera are represented in the British flora.

The plants are herbs, sometimes annual as in pimpernel (*Anagallis arvensis*), but generally perennial as in *Primula*, where the

plant persists by means of a sympodial rhizome, or in *Cyclamen* by means of a tuber formed from the swollen hypocotyl. The leaves form a radical rosette as in *Primula* (primrose, cowslip, etc.), or there is a well-developed aerial stem which is erect, as in species of *Lysimachia*, or creeping, as in *Lysimachia Nummularia* (creeping jenny or money-wort). *Hottonia* (water violet) is a floating water plant with submerged leaves cut into fine linear segments. The leaves are generally simple, often with a toothed margin; their arrangement is alternate, opposite or whorled. The flowers are solitary in the leaf-axils as in pimpernel, money-wort, etc., or umbelled as in primrose, where the umbel is sessile, and cowslip, where it is stalked, or in racemes or spikes as in species of *Lysimachia*. Each flower is subtended by a bract, but there are no bracteoles, and corresponding with the absence of the latter the two first developed sepals stand right and left. The flowers are hermaphrodite and regular with parts in fives (pentamerous) throughout, though exceptions from the pentamerous arrangement occur. The sepals are leafy and persistent; the corolla is generally divided into a longer or shorter tube and a limb which is spreading, as in primrose, or reflexed, as in *Cyclamen*; in *Soldanella* it is bell-shaped; in *Lysimachia* the tube is often very short, the petals appearing almost free; in *Glaux* the petals are absent. The five stamens spring from the corolla-tube and are opposite to its lobes; this anomalous position is generally explained by assuming that an outer whorl of stamens opposite the sepals has disappeared, though sometimes represented by scales as in *Samolus* and *Soldanella*. The superior ovary—half-inferior in *Samolus*—bears a simple style ending in a capitate entire stigma, and contains a free-central placenta bearing generally a large number of ovules, which are exceptional in the group Symptetales in having two integuments. The fruit is a capsule dehiscing by five, sometimes ten, teeth or valves, or sometimes transversely (a pyxidium) as in *Anagallis*.

Cross pollination is often favoured by dimorphism of the flower, as shown in species of *Primula*. The two forms have long and short styles respectively, the stamens occupying corresponding positions half-way down or at the mouth of the corolla-tube; the long-styled flowers have smaller pollen-grains, which correspond with smaller stigmatic papillae on the short styles (*see PRIMROSE*).

The family is divided into five tribes by characters based on the presence or absence of tubers, the regularity of the flower, the aestivation of the corolla, etc. The ovules are generally semi-anatropous so that the seed is peltate with the hilum in the centre on one side (or ventral), but sometimes, as in *Hottonia* and *Samolus*, anatropous with the hilum basal—together with the method of dehiscence of the capsule and the relative position of the ovary. The chief British genera are *Primula*; and the *Lysimachia*, loose-strife, including *L. Nummularia*, money-wort; *Anagallis*, pimpernel; and *Hottonia*, water violet. The most familiar American genera are *Primula* (primrose), *Samolus* (water pimpernels and brookweeds), *Lysimachia* (loose-strife), and *Dodecatheon* (shooting stars or American cowslips).

For further details see A. Engler and K. Prantl, *Die Natürlichen Pflanzenfamilien* (Leipzig, 1887–1908); A. B. Rendle, *Classification of Flowering Plants* (Cambridge, 1925).

**PROTEACEAE**, a family of dicotyledonous plants comprising about 50 genera and some 960 species, of which about 600 are Australian, including the silky oak (*Grevillea robusta*) introduced into Ceylon for shade and timber, and the Australian honey-suckles (*Banksia*); there are about 260 species in south-western Cape Colony, including the silver tree (*Leucadendron argenteum*); the remaining species have a wide but irregular distribution in Asia, Africa, America and Australasia. Most of the species are trees or shrubs, and the majority are xerophytic (*i.e.*, inhabit arid country).

**RANUNCULACEAE**, in botany, a family of Dicotyledons belonging to the series Ranales, and containing 40 genera with about 700 species, which are distributed through temperate and cold regions but occur more especially in the northern hemisphere. It is generally regarded as a genetic family which gave rise to the higher Dicotyledons, as well as the Monocotyledons. It contains many well known forms, such as buttercup, larkspur,



anemone, columbine, clematis, marsh marigold, peony, etc. It is well represented in Britain, where 12 genera are native. In North America there are about 25 genera. The plants are mostly herbs, rarely shrubby, as in *Clematis*, which climbs by means of the leaf-stalks, with alternate leaves, opposite in *Clematis*, generally without stipules. The flowers, which show considerable variation in the number and development of parts, are characterized by free hypogynous sepals and petals, numerous free stamens, usually many free one-celled carpels and small seeds containing a minute straight embryo embedded in a copious endosperm. The parts of the flower are generally arranged spirally on a convex receptacle. The fruit is one-seeded, an achene or a many-seeded follicle, rarely, as in *Actaea*, a berry.

The family falls into several well-defined tribes which are distinguished by characters of the flower and fruit; all are represented among British native or commonly grown garden plants.

**Tribe I. Paeonieae**, peony group, are mostly herbs with deeply cut leaves and large solitary showy flowers in which the parts are spirally arranged, the sepals, generally five in number, passing gradually into the large coloured petals. There are 2–5 free carpels which bear a double row of ovules along the ventral suture. There are no honey-leaves (nectaries) but honey is secreted by a ring-like swelling round the base of the carpels, which become fleshy in the fruit and dehisce along the ventral suture. There are only three genera, the largest of which, *Paeonia*, occurs in Europe, temperate Asia and western North America. *P. officinalis* is the common peony.

**Tribe II. Helleboreae** are almost exclusively north temperate or subarctic. The plants are herbs, either annual, e.g., *Nigella* (love-in-a-mist), or perennial by means of a rhizome, as in *Aconitum* or *Eranthis* (winter aconite). The leaves are simple, as in *Caltha*, but more often palmately divided as in hellebore, aconite and larkspur. The flowers are solitary (*Eranthis*) or in cymes or racemes, and are generally regular as in *Caltha* (king-cup, marsh marigold), *Trollius* (globe-flower), *Helleborus* (hellebore), *Aquilegia* (columbine); sometimes markedly irregular as in *Aconitum* (aconite) and *Delphinium* (larkspur). The carpels, generally three to five in number, form in the fruit a many-seeded follicle, except in *Actaea* (baneberry), where the single carpel develops to form a many-seeded berry, and in *Nigella*, where the five carpels unite to form a five-chambered ovary. There is considerable variety in the form of the floral envelopes and the arrangement of the parts. The outer series, or sepals, generally five in number, is generally white or bright-coloured. Thus in *Caltha* and *Trollius* the sepals form a brilliant golden-yellow cup or globe, and in *Eranthis* a pale yellow star which contrasts with the green involucre of bracts immediately below it; in *Nigella* they are blue or yellow, and also coloured in *Aquilegia*. In *Helleborus* the greenish sepals persist till the fruit is ripe. *Aconitum* and *Delphinium* differ in the irregular development of the sepals, the posterior sepal being distinguished from the remaining four by its helmet-shape (*Aconitum*) or spur-shape (*Delphinium*). In *Caltha* there are no petals, but in the other genera there are honey-secreting and storing structures varying in number and in form in the different genera. In *Trollius* they are long and narrow with a honey-secreting pit at the base, in *Nigella* and *Helleborus* they form short-stalked pitchers, in *Aquilegia*, they are large and coloured with a showy petal-like upper portion and a long basal spur in the tip of which is the nectary. In *Delphinium* they are also spurred, and in *Aconitum* form a spur-like sac on

a long stalk. The parts of the flower are generally arranged in a spiral (acyclic), but are sometimes hemicyclic, the perianth forming a whorl as in winter aconite; rarely is the flower cyclic, as in *Aquilegia*, in which case the parts throughout are arranged in alternating whorls. In *Caltha*, where there are no petals, honey is secreted by two shallow depressions situated on the side of each carpel.

**Tribe III. Anemoneae**, are chiefly north temperate, Arctic and alpine plants, but also pass beyond the tropics to the southern hemisphere. They differ from the two preceding tribes in the numerous carpels, each with only one ovule, forming a fruit of numerous achenes. They are annual or perennial herbs, erect as in *Anemone*, *Thalictrum* (meadow-rue) and many buttercups, or creeping as in *Ranunculus repens*; the section *Batrachium* of the genus *Ranunculus* (q.v.) contains aquatic plants with submerged or floating stems and leaves. The flowers are solitary, as in *Anemone Pulsatilla* (Pasque flower), or cymose as in species of *Ranunculus*, or in racemes or panicles as in *Thalictrum*. The parts are spirally arranged throughout as in *Myosurus* (mouse-tail), where the very numerous carpels are borne on a much elongated receptacle, *Adonis* (pheasant's eye), or the perianth is whorled as in *Anemone* and *Ranunculus*. In *Anemone* and *Thalictrum* there is only one series of perianth leaves, which are petaloid and attractive in *Anemone* where honey is secreted by modified stamens, as in *A. Pulsatilla*, or, as in *A. nemorosa* (wood anemone), there is no honey and the flower is visited by insects for the sake of the pollen; in *Thalictrum* the perianth is greenish or slightly coloured, and the flower is wind-pollinated (*T. minus*) or visited for its pollen. In *Ranunculus* and *Adonis* a calyx of green protective sepals is succeeded by a corolla of showy petals; in *Ranunculus* there is a basal honey-secreting gland which is absent in *Adonis*. In *Anemone* the achenes bear the persistent naked or bearded style which aids in dissemination; the same purpose is served by the prickles on the achenes of *Ranunculus arvensis*. *Clematis* (q.v.), is characterized by its shrubby, often climbing habit, opposite leaves and the valvate, not imbricate as in the other tribes, aestivation of the sepals. The usually four sepals are whorled and petaloid, the numerous stamens and carpels are spirally arranged; the flowers are visited by insects for the sake of the abundant pollen. The fruit consists of numerous achenes which are generally prolonged into the long feathery style, whence the popular name of the British species, old man's beard (*Clematis vitalba*).

Special articles will be found on the more important genera of Ranunculaceae, e.g., ACONITE, ADONIS, ANEMONE, BANEERRY (*Actaea*), CLEMATIS, COLUMBINE, HELLEBORE, RANUNCULUS. For further details see A. Engler and K. Prantl, *Die Natürlichen Pflanzenfamilien* (Leipzig, 1887–1908); A. B. Rendle, *Classification of Flowering Plants* (Cambridge, 1925).

**RESEDACEAE**, in botany, the mignonette family, dicotyledonous plants, mostly xerophytic herbs. There are six genera and about 60 species. *Reseda odorata* is the mignonette (q.v.); *R. lutea* is dyer's woad. (See WOAD.)

**RUBIACEAE**, in botany, a large family of seed plants, belonging to the series Rubiales of the subclass Sympetalae (Gamopetalae) of dicotyledons, and containing about 450 genera with about 5,500 species. It is mainly a tropical family of trees, shrubs and herbs, but some of the tribes, especially Galieae, to which the British representatives belong and which contains only herbs, are more strongly developed in temperate regions; some species of *Galium* reach the Arctic zone.

The most striking characteristic of the family are the opposite-decussate, generally entire, stipulate leaves. The stipules are very varied in form; they generally stand between the petioles of a pair of leaves (interpétiole). The two stipules of adjacent leaves are usually united, and in the Galieae, as well shown in the British species, are enlarged and leaf-like, forming with the two leaves an apparent whorl; by fusion or branching of the stipules the number of leaves in the whorl varies from four to eight or more. The flowers are mostly arranged in cymes or panicles or crowded into heads, and are frequently showy. The flowers are hermaphrodite and regular with parts in fours or fives; the four or five sepals, petals and stamens are placed above the ovary, which consists of two carpels and is crowned by a simple style usually ending in a



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GLOBE FLOWER (TROLLIUS EURO-  
PAEUS)



head or in two lobes. The sepals are often small, sometimes reduced to a narrow ring encircling the top of the ovary or altogether absent. The united petals form a corolla which varies widely in form in the different genera; it is often funnel- or salver-shaped. The stamens are fixed to the corolla-tube and alternate in position with its segments; the flowers are often dimorphic (or heterostyled) with short-styled and long-styled forms.

The fruit also varies widely in form and is dry or fleshy. When dry it forms a capsule with septicidal or loculicidal dehiscence or is a schizocarp separating when dry into two one-seeded mericarps which, as in the British cleavers (*Galium Aparine*), sometimes bear hooked appendages which aid their dispersal.

The family is divided into a large number of tribes based on the number of ovules in each ovary-chamber, the character of the fruit seed and ovule, and the aestivation of the corolla. These may be arranged in two classes as follows:—

*Cinchonoideae*, often woody plants with scale-like stipules, and numerous ovules in each ovary-chamber; the fruit is generally a capsule. To this belong *Cinchona* (*q.v.*), a genus of large trees with handsome flowers containing about 40 species in the Andes of South America—it is well known as a source of quinine. An allied genus, *Bouvardia* (*q.v.*), is cultivated for its flowers.

*Coffeoidae*, often woody or shrubby plants with scale-like stipules; each ovary-chamber contains only a single ovule. *Coffea*, a genus of shrubs with about 45 species in the Old World tropics, includes the coffee plant (*C. arabica* and *C. liberica*); the fruit is a two-seeded drupe, the seed is the "coffee-bean." The thickened root of *Uragoga Ipecacuanha* yields ipecacuanha. In this class is the tribe *Stellateae*, herbaceous plants with leaf-like stipules; each ovary-chamber contains one ovule only. Includes the four British genera: *Rubia*, one species of which, *R. tinctorum*, is madder; *Galium*, including *G. verum* (lady's bedstraw), *G. Aparine* (goose-grass or cleavers), and other British species; *Asperula*, including *A. odorata* (woodruff) and *Sherardia*.

The most common representatives in eastern North America are *Galium* (cleavers, goose grass, wild licorice, etc.), *Houstonia* (bluets, innocence), and *Mitchella* (partridge berry). In western North America, in addition to a few species of *Galium*, the genus *Kelloggia* is very characteristic.

**RUTACEAE**, a family of dicotyledonous plants, mostly shrubs and trees, comprising about 100 genera and 800 species found in temperate and tropical regions, and especially abundant in Australia and South Africa. *Ruta graveoleus* is rue (*q.v.*). *Citrus* includes the grapefruit, orange, lemon (*qq.v.*), etc. *Chloroxylon Swietenia* is satinwood (*q.v.*). *Ptelea trifoliata* is the shrubby trefoil or wafer-ash (*q.v.*); *Zanthoxylum americanum* is the prickly-ash (*q.v.*).

**SANTALACEAE**, in botany, the sandalwood family, dicotyledonous, semi-parasitic shrubs, trees and herbs of tropical and temperate regions. There are 26 genera and about 250 species. *Santalum album* is the true sandalwood (*q.v.*). The bastard toad-flax (*Thesium humifusum*), an herbaceous root-parasite with green leaves, native to Great Britain, belongs to this family. To it belong the North American species of *Comandra*, likewise called bastard toad-flax and sometimes parasitic, and also the oil-nut or buffalo-nut (*Pyrularia pubera*), of the Appalachian region.

**SAPOTACEAE**, a family of tropical dicotyledonous plants, most of which are trees with leathery leaves. There are 35 genera and about 600 species, many of which are of economic importance as sources of gutta-percha (*q.v.*), balata, shea butter, ironwood, etc. *Chrysophyllum Cainito* is the West Indian star-apple. *Mimusops elata* is the Brazilian milk-tree (*q.v.*). *Sapota Achras* yields the luscious sapodilla or naseberry and the elastic gum chicle (*q.v.*). *Achras Zapota*, of Central America, is the sapote or marmalade-plum. *Lucuma nervosa* is the egg-fruit or canistel, of South America, now naturalized in Florida and the West Indies.

**SAPROPHYTES**, the name given in botany to plants which grow upon decaying organic matter, the products of the decay of which they absorb. Many fungi (*q.v.*) are saprophytic, as are some orchids (*q.v.*) and other flowering plants.

**SAXIFRAGACEAE**, in botany, a small family of dicotyle-

done belonging to the sub-class Archichlamydeae and the cohort Rosales. There are ninety genera with about 750 species distributed through the Arctic and north temperate zone, often alpine. It is represented in Britain by its largest genus *Saxifraga* (see SAXIFRAGE), *Chrysosplenium* (golden saxifrage) and *Parnassia* (grass of Parnassus). The plants are herbs, generally with scattered exstipulate leaves with a broad leaf-base. The small flowers are generally arranged in cymose inflorescences and are bisexual, regular and hypogynous, perigynous or more frequently more or less epigynous, this variation in the relative position of the ovary occurring in one and the same genus *Saxifraga*. The free stamens are obdiplostemonous, *i.e.*, those of the outer whorl are opposite to the petals, and two carpels. The carpels are sometimes free, more generally united at the base, or sometimes completely joined to form a one- or two-chambered ovary with two free styles. The fruit is a many-seeded capsule.

Nearly half the species (350) are contained in the genus *Saxifraga*. *Chrysosplenium*, with 45 species, two of which are British, has a very similar distribution. The North American genus *Heuchera* has sometimes apetalous flowers. *Astilbe* has 20 species in temperate Asia and north-eastern North America; *A. japonica* is commonly grown in the spring as a pot-plant, and often misnamed *Spiraea*.

The family is now extended to include other groups of genera differing in habit and more or less in general conformation from those referred to. Among these is the genus *Ribes*, to which belong the gooseberry (*R. Grossularia*) and currants of gardens. These are shrubs with racemes of flowers which have only one whorl of stamens (isostemonous), an inferior unilocular ovary with two parietal placentas, and fruit a berry. Other genera are *Hydrangea* (*q.v.*), *Deutzia* and *Philadelphus*, all well-known garden plants; *P. coronarius* is the so-called syringa or mock-orange. They are shrubs or trees with simple generally opposite leaves, pentamerous flowers with epigynous stamens and a tri- to pentalocular ovary. *Escallonia*, which represents a small group of genera with leathery gland-dotted leaves, is also included.

In North America, *Saxifraga* is represented by about 30 species, the other prominent genera being *Ribes* (currant and gooseberry) with 20 species, and *Heuchera* (alum root) with 10 species.

For further details see A. Engler and K. Prantl, *Die Natürlichen Pflanzenfamilien* (Leipzig, 1887-1908); A. B. Rendle, *Classification of Flowering Plants* (Cambridge, 1925).

**SCROPHULARIACEAE**, in botany, a family of seed plants belonging to the sympetalous section of Dicotyledons and a member of the series Tubiflorae. It is a cosmopolitan order containing about 200 genera with about 2,600 species; the majority occur in temperate regions, the numbers diminishing rapidly towards the tropics and colder regions. About 30% of the species are annual herbs, such as eyebright (*Euphrasia officinalis*), cow-wheat (*Melampyrum*), and species of *Veronica*; more than 60% are biennial or generally perennial herbs and undershrubs, such as species of *Veronica*, mullein (*Verbascum*), foxglove (*Digitalis purpurea*), etc., while shrubs and trees are rare; *Paulownia*, a native of the mountains of Japan, a tree with large leaves and handsome panicles of violet flowers, is grown in European gardens.

The stem is sometimes prostrate and creeping, as in ivy-leaved toad-flax (*Linaria Cymbalaria*) and some of the native British Veronics, but generally erect as in foxglove, figwort, mullein, etc.; a few are climbers as *Rhodochiton* and *Maurandia*. The South African genera *Hyobanche* and *Harveya* are parasites almost devoid of chlorophyll with scale-like leaves; and many genera are semiparasitic, having green leaves, but attaching themselves by root-suckers to roots of grass, etc., from which they derive part of their nourishment; such are *Euphrasia*, *Rhinanthus*, *Pedicularis*, etc. A few genera are aquatic, *e.g.*, *Ambulia* (Old World Tropics), and have much divided submerged leaves and entire aerial leaves. The flowers are solitary in the leaf-axils, as in *Mimulus*, species of *Linaria*, etc., or form spikes or racemes which are terminal as in foxglove, species of *Veronica*, etc., or axillary, as in *Veronica* (*Chamaedrys* section). The flowers are hermaphrodite, hypogynous and zygomorphic in the median plane, being often more or less two-lipped, and having five sepals joined below and persist-



ing in the fruiting stage, five petals uniting to form a corolla of various shape, generally four stamens, the fifth (posterior) being suppressed or represented by a rudiment, while the anterior pair are longer than the posterior, and two generally equal carpels in the median plane forming a two-celled ovary containing numerous anatropous ovules on a thick axile placenta, and bearing a simple or bilobed style.

When a terminal flower is present it becomes regular as in toad-flax, where radial symmetry is produced by development of a spur to each petal—such flowers are termed peloric; all the flowers in a spike are sometimes peloric. In *Euphrasia* and many species of *Veronica* the posterior sepal is suppressed. The form of the corolla shows great variety, depending on the length and breadth of the tube—which in *Veronica* is almost obsolete, while in foxglove it is large and almost bell-shaped—and the development of the limbs, which are spreading in *Veronica*, small and almost erect in figwort, or form a pair of closed lips as in *Linaria* and *Antirrhinum*. In *Verbascum* the five segments are almost equal, forming a nearly regular corolla; the approach to regularity in the corolla in *Verbascum* is associated with the presence of five fertile stamens, but the three posterior are generally larger than the two anterior. In *Veronica*, *Calceolaria* and other genera only two stamens are present. Honey is secreted by a disk surrounding the base of the ovary or by special nectaries below it. *Verbascum* and *Veronica* with a short-tubed corolla represent an open type of flower with more exposed nectar; in foxglove the honey is at the base of the long tube, and a bee crawling to reach it will rub with its back the anthers or stigmas which are placed on the upper side of the bell. The closed flowers of *Linaria* and *Antirrhinum* can be visited only by insects strong enough to separate the lips.

The fruit is generally a capsule surrounded at the base, or sometimes as in yellow-rattle (*Rhinanthus*) enveloped in the persistent calyx; it opens by two or four valves, or, as in *Antirrhinum*, by pores. Occasionally it is a berry. In *Linaria Cymbalaria* the fruit becomes buried by the stalks bending downwards when ripe.

The family is divided into tribes by characters derived from the number of fertile stamens present and the form of the corolla. It is well represented in Britain by 13 genera, viz., *Verbascum* (mullein), *Linaria* (toad-flax), *Antirrhinum* (snapdragon), *Scrophularia* (figwort), *Limosella*, *Sibthorpia*, *Digitalis* (foxglove), *Veronica* (speedwell), *Bartsia*, *Euphrasia* (eyebright), *Rhinanthus* (yellow-rattle), *Pedicularis* (louse-wort) and *Melampyrum* (cow-wheat). The best known representatives in North America are *Verbascum* (mullein), *Pentstemon* (beard-tongue), *Mimulus* (monkey-flower), *Veronica* (speedwell), *Gerardia*, *Castilleja* (painted cup), and *Pedicularis* (louse-wort). Common in cultivation are European species of *Antirrhinum* (snapdragon), *Digitalis* (foxglove), and *Linaria* (toad-flax). Several genera are well known in gardens; such are *Calceolaria*, *Collinsia*, *Pentstemon* and *Mimulus* (musk).

**SOLANACEAE**, in botany; a family of dicotyledons belonging to the sub-class Sympetalae (or Gamopetalae) and to the series Polemoniales, containing 72 genera with about 1,750 species, widely distributed through the tropics, but passing into the temperate zones. The chief centre of the family lies in Central and South America; 36 of the genera are endemic in this region. It is represented in Britain by three genera including four species: *Hyoscyamus niger* (henbane), *Solanum Dulcamara* (bittersweet) and *S. nigrum* and *Atropa Belladonna* (deadly nightshade).

It is represented in North America by about 40 species, the conspicuous genera being *Solanum* (nightshade, bittersweet, horse nettle), *Physalis* (ground cherry), and *Datura* (jimson weed). *Nicotiana* (tobacco) is represented by two species, one extending from Colorado to Nevada and California, and the other a native of Oregon, but cultivated by the Indians eastward to the Missouri river. The plants are herbs, shrubs or small trees. *Solanum nigrum*, a common weed in waste places, is a low-growing annual herb; *S. Dulcamara* is an irregularly climbing herb perennial by means of a widely creeping rhizome; *Atropa Belladonna* is a large perennial herb. The genus *Solanum*, to which belong more than half the species in the family, contains plants of very various habits including besides herbs, shrubs and trees. The leaves are generally

alternate, but in the flower-bearing parts of the stem are often in pairs, an arrangement which, like the extra-axillary position of the flowers or cymes, results from a congenital union of axes.

In *Atropa Belladonna* one of the branches at each node is undeveloped and there is a pair of unequal leaves; the smaller subtends the branch which has not developed, the larger has been carried up from the node below.



FROM "MEDIZINAL PFLANZEN" (KOEHLER)

THORN-APPLE OR JIMSON-WEED (*Datura stramonium*), A COARSE ANNUAL PLANT OF THE NIGHTSHADE FAMILY (SOLANACEAE). FOUND WIDELY IN RICH SOILS IN TEMPERATE AND TROPICAL REGIONS

The hermaphrodite, generally regular, flowers have the parts in fives, five sepals, five petals, five stamens in alternating whorls, and two carpels, which are generally placed obliquely. The corolla is regular and rotate as in *Solanum nigrum*, or bell-shaped as in *Atropa*, or somewhat irregular as in *Hyoscyamus*; in the tribe Salpiglossideae, which forms a link with the closely allied family Scrophulariaceae (*q.v.*), it is zygomorphic, forming *e.g.*, as in *Schizanthus*, a two-lipped flower. The stamens are inserted on the corolla tube and alternate with its lobes; in zygomorphic flowers only two or four fertile stamens are present. The flowers are generally conspicuous and honey is secreted on the disk at the base of the ovary or at the bottom of the corolla tube between the stamens. The ovary is usually bilocular, but in *Capsicum* becomes unilocular above, while in some cases an in-growth of a secondary septum makes it 4-celled as in *Datura*, or irregularly 3- to 5-celled as in *Nicandra*. The anatropous ovules are generally numerous on swollen axile placentae. The style is simple and bears a bilobed or capitate stigma. The fruit is a many-seeded berry, as in *Solanum*, or capsule, as in *Datura*, where it splits lengthwise, and *Hyoscyamus*, where it opens by a transverse lid forming a pyxidium. The embryo is bent or straight and embedded in endosperm. The persistent calyx may serve to protect the fruit or aid in its distribution, as in the red bladdery structure enveloping the fruit of *Physalis*.

The family is divided into five tribes after Wettstein; the division is based on the greater or less curvature of the embryo, the number of ovary cells and the regular or zygomorphic character of the flower. The great majority of the genera belong to the tribe Solaneae, which is characterized by a two-celled ovary. *Lycium* is a genus of trees or shrubs, often thorny, with a juicy berry; *L. chinense* (*L. barbarum*) is a straggling climber often cultivated under the name of tea-plant. For *Atropa*, see NIGHTSHADE; for *Hyoscyamus*, see HENBANE. *Physalis*, with 50 species mostly in the warmer parts of North and South America, includes *P. alkekengi*, "winter cherry," and *P. peruviana*, "Cape gooseberry." *Capsicum* (*q.v.*) is widely cultivated for its fruit, which are the



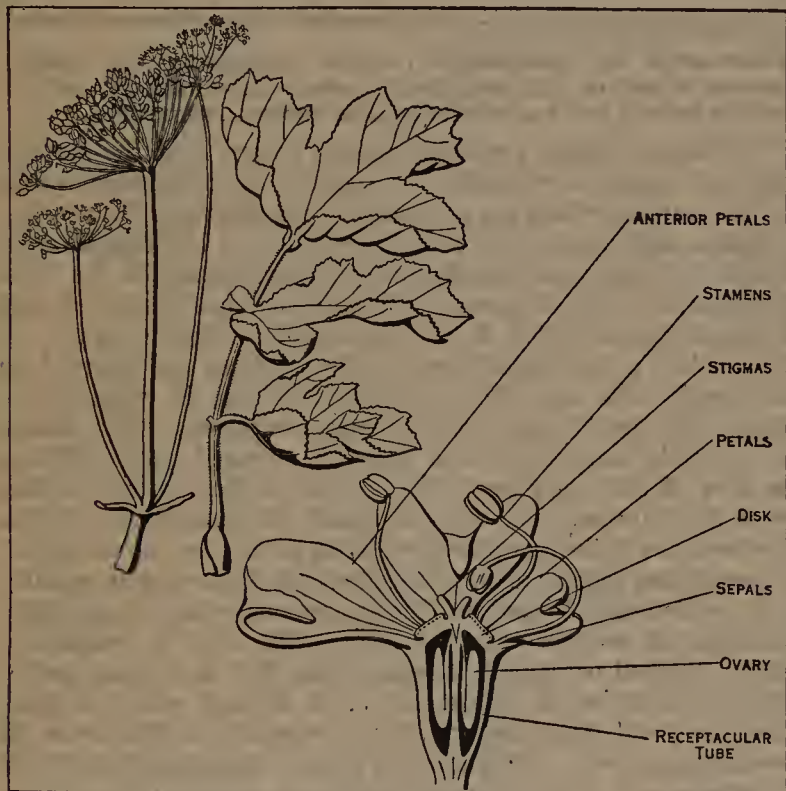
so-called chillies. *Lycopersicon esculentum* is the tomato (*q.v.*) and *L. pimpinellifolium* is the currant-tomato; both are native to western South America, as is also *Cyphomandra betacea*, the tree-tomato. For *Mandragora*, see MANDRAKE. To the tribe *Datureae*, characterized by a four-celled ovary, belongs *Datura*; *D. Stramonium* (thorn-apple), sometimes found as an escape in Britain, is officinal. *D. Metel*, native to India, and *D. meteloides*, of the south-western United States, are large-flowered annuals, grown in gardens in warm-temperate countries, as are the tree-like shrubs, *D. sanguinea*, native to Peru; *D. suaveolens*, native to Brazil, and *D. arborea*, of the central Andes. *Nicotiana*, to which belong the tobacco plant (*N. tabacum*) and other cultivated species, and *Petunia*, are American genera belonging to the tribe *Cestreae*, in which the embryo is straight or only slightly bent, as it is also in the tribe *Salpiglossideae*; *Salpiglossis* and *Schizanthus* are known in cultivation.

Among other plants of the family grown for ornament are the pepino (*Solanum muricatum*), Jerusalem-cherry (*S. Pseudo-Capsicum*), scarlet eggplant (*S. integrifolium*), tomatillo (*Physalis ixocarpa*) and strawberry-tomato (*P. pubescens*).

Numerous plants of the family are narcotic-poisonous, especially species of *Solanum* (nightshade), *Atropa* (belladonna), *Hyoscyamus* (henbane) and *Datura* (stramonium).

**SPERMOPHYTA**, the name often used in botany to denote the seed-plants, including the true flowering plants, or angiosperms (*q.v.*), and the conifers and their allies or gymnosperms (*q.v.*).

**UMBELLIFERAE**, in botany, a family of polypetalous dicotyledons belonging to the order Umbelliflorae, which includes also the families Araliaceae (ivy family) and Cornaceae (dogwood family). It contains 200 genera with about 2,700 species, occurring in all parts of the world but chiefly in north temperate regions. It is well represented in the British flora by 35 genera.



FROM GROOM, "ELEMENTARY BOTANY" (G. BELL & SONS, LTD.)

LEAF AND INFLORESCENCE (COMPOUND UMBEL) OF COW PARSNIP (*HERACLEUM DUBIUM*), ALSO CROSS-SECTION OF MARGINAL ZYGOMORPHIC FLOWER

The plants are annual or perennial herbs, rarely shrubby as sometimes in *Bupleurum*, with generally a very characteristic habit, namely stout erect stems with hollow internodes, alternate pinnately compound exstipulate sheathing leaves and compound umbels of small, generally white, flowers.

An example of an annual is the common fool's parsley, *Aethusa Cynapium*; carrot (*Daucus Carota*) is a biennial; others are perennial, persisting by means of tubers or rhizomes—such are hogweed (*Heracleum*), *Angelica*, *Peucedanum*, and others. Some genera have a creeping stem as in *Hydrocotyle* (pennywort), a small herb with a creeping filiform stem and, in the British species,

entire leaves. *Bupleurum* has simple, entire, often perfoliate leaves. *Azorella*, a large genus in south temperate regions, has a peculiar caespitose habit, forming dense cushions often several feet in diameter and persisting for many years; they resemble those of the Australian *Raoulia* (vegetable sheep). *Eryngium*, represented in Britain by sea-holly (*E. maritimum*), is a large genus of rigid often glaucous herbs with spiny-toothed leaves, which in some South American species with narrow parallel-veined blade and broadly sheathing base recall those of a monocotyledon such as *Agave* or *Bromelia*. In sanicle (*Sanicula*), *Astrantia* and others the leaves are palmately divided.

There is also considerable variety in the development of the umbel, which is usually compound but sometimes simple, as generally in *Hydrocotyle* and *Astrantia*, rarely reduced to a single flower as in species of *Hydrocotyle*. In *Eryngium* the flowers are crowded into dense heads subtended by a whorl of rigid bracts. A terminal flower, distinguished by its form and dark colour, is sometimes present as in carrot (*Daucus*). The presence or absence of bracts and their form when present afford useful diagnostic characters. When present at the base of the primary rays of the umbel they form the *involucre*, and the *involucel* when at the base of a partial umbel. In *Astrantia* the simple umbel is enveloped by a large, often coloured, involucre.

The small epigynous flowers are usually hermaphrodite and regular, with parts in fives. The sepals are usually very small, often represented only by teeth on the upper edge of the ovary; the petals are usually obovate or obcordate in shape, often with the tip inflexed; the stamens have long slender filaments bent inwards in the bud but ultimately spreading; the two carpels are in the median plane; the two-celled ovary is surmounted by an epigynous glandular disk, which bears the two styles. Each ovary-cell contains a single pendulous anatropous ovule with a ventral raphe and a single integument. The flowers are rendered conspicuous by being massed into more or less dense flat-topped inflorescences (umbels). A resemblance to the rayed heads of *Compositae* is suggested in the frequently larger size of the flowers on the circumference of the umbel which are often sterile and zygomorphic from the larger size of the outer petals. This arrangement allows a large number of flowers to be visited by insects in a short time. The flowers are generally white, sometimes pink or yellow, very rarely blue; they are generally scented, but the whole plant has an odour from the general presence in the tissues of an ethereal oil or resin. The flower is widely open, the petals and stamens radiating from the central disk, on which honey is secreted, and is thus accessible to short-tongued flies. Cross-pollination is necessary, the flowers being generally protandrous.

The fruit is very characteristic; a schizocarp which splits down the septum to form two dry one-seeded mericarps which are at first attached to, or pendulous from, an entire or split central axis or *carpopore*. The form of the mericarp affords valuable characters for distinguishing genera. On the outer surface of each are generally five ridges (primary ridges), between which are sometimes four secondary ridges; oil-cavities, *vittae*, are often present in the intervening furrows.

The family is classified according to the nature of the flower and fruit. Engler divides the family into three main classes, *Hydrocotyloideae*, *Saniculoideae*, *Apioideae*; the first two with two subfamilies each, the last with eight. The 35 British genera represent seven of the twelve subfamilies. The following may be mentioned: *Hydrocotyle* (pennywort), *Sanicula* (sanicle), *Conium* (hemlock, *q.v.*), *Smyrniium* (Alexanders), *Apium* (celery, *q.v.*), *Carum* (caraway, *q.v.*), *Myrrhis* (cicely), *Foeniculum* (fennel, *q.v.*), *Aethusa* (fool's parsley, *q.v.*), *Angelica* (*q.v.*), *Pastinaca* (parsnip, *q.v.*), *Heracleum* (hogweed), *Daucus* (carrot).

It is represented in North America by about 70 genera. The more common ones are *Sanicula* (black snakeroot), *Osmorrhiza* (sweet cicely), *Cicuta* (water hemlock), *Sium* (water parsnip), *Thaspium* (meadow parsnip), and *Angelica*.

For further details see Engler & Prantl, *Die Natürlichen Pflanzenfamilien* (Leipzig, 1887-1908); J. C. Willis, *Flowering Plants and Ferns* (Cambridge, 1925); A. B. Rendle, *The Classification of Flowering Plants* (Cambridge, 1925).



**URTICACEAE** (nettle family), in botany, a family of flowering plants belonging to the order Urticales, which includes also Ulmaceae (elm family), Moraceae (mulberry, fig, etc.) and Cannabaceae (hemp and hop). It contains 41 genera, with about 480 species, mainly tropical, though several species such as the common stinging nettle (*Urtica dioica*) are widely distributed and occur in large numbers in temperate climates. Two genera are represented in the British Isles, *Urtica* (see NETTLE) and *Parietaria* (pellitory, *q.v.*). In addition to *Urtica* and *Parietaria*, four other genera,—*Boehmeria*, *Hesperocnide*, *Laportea* and *Pilea*, are represented in North America, with some 15 native species.

The plants are generally herbs or somewhat shrubby, rarely, as in some tropical genera, forming a bush or tree. The simple, often serrated, leaves have sometimes an alternate sometimes an opposite arrangement and are usually stipulate—exstipulate in *Parietaria*. Stinging hairs often occur on the stem and leaves. The bast-fibres of the stem are generally long and firmly attached end to end, and hence of great value for textile use. Thus in ramie (*q.v.*, *Boehmeria nivea*) a single fibre may reach nearly 9 in. in length, and in stinging nettle as much as 3 in. *Maoutia* and *Urtica* have also been used as sources of fibre. The small inconspicuous regular flowers are arranged in definite (cymose) inflorescences often crowded into head-like clusters. They are unisexual and monoecious or dioecious. The four or five green perianth leaves (or sepals) are free or more or less united; the male flowers contain as many stamens, opposite the sepals. The flowers are adapted for wind-pollination. The female flower contains one carpel bearing one style with a brush-like stigma and containing a single erect ovule. The fruit is dry and one-seeded; it is often enclosed within the persistent perianth. The family is divided, according to Engler,



COMMON NETTLE, (*URTICA DIOICA*)

### PUBLISHERS' NOTE

Since the publication of the New 14th Edition of the Encyclopaedia Britannica, we have received thousands of requests to publish in separate form the articles in certain fields of knowledge so that these articles may be the more available for continuous reading, for students' use, etc. Accordingly we have prepared booklets containing all the Britannica articles on Painting; Mammals and Birds; Chinese Art; Botany, the Science; Botany: Plants and Gardening; The Earth, the Seas and the Heavens; Japanese Art; Fishes, Reptiles and Insects; The Theatre and Motion Pictures; Graphic Arts; and expect to follow these with many others. We trust they will prove useful, not only in themselves but also as evidence of the wide scope and the fullness of information in the Britannica itself.

The articles in this booklet are all taken *verbatim* from the New 14th Edition of the Encyclopaedia Britannica except that material not essential to the subject has been omitted and in a few unimportant instances certain material has been condensed for mechanical reasons. The plates, too, are reproduced unchanged but the numbering is not always consecutive because the original numbering in the Britannica has been retained in order to agree with the text.

into two main classes: (1) the *Urereae* with stinging hairs, including the genera *Urtica*, *Urera*, *Laportea*, and (2) others, which are without stinging hairs.

**VERBENACEAE**, a family of dicotyledonous plants, comprising about 70 genera and some 750 species of herbs, shrubs and trees, nearly all tropical and subtropical. Vervain (*q.v.*) is British. *Lippia* and *Cymbopogon* yield verbena oil and several species, as teak (*Tectona grandis*), supply useful timber. Many are lianes. Some species bear thorns; others are xerophytic. Numerous species are cultivated for ornament, as the verbena (*q.v.*), chaste-tree (*Vitex Agnus-castus*), glory-bower (*Clerodendrum*), purple wreath (*Petreaea volubilis*), golden dewdrop (*Durandtia repens*), bluebeard (*Caryopteris incana*) and French mulberry (*Callicarpa americana*).

**WELWITSCHIA:** see GYMNOSPERMS.

**PALAEOBOTANY** or **VEGETABLE PALAEONTOLOGY**, a branch of the science of botany, is concerned with the study of plants which lived in past ages, by means of their remains found as fossils in the rocks. Fossil plants may be regarded as the documents on which the history of the plant-world is founded. A surprising amount is known about the form of fossil plants from rocks as ancient as those of the Ordovician (see GEOLOGY), and, according to the latest estimates of geological time, about 500,000,000 years have since elapsed. During that time the constitution of the flora of the earth has been changing continuously. Starting with the fossils found in the older sedimentary rocks and reviewing those of successively later formations, it becomes apparent that each species, genus, or larger systematic grouping has three phases in its history: its first appearance and development, its period of maximum abundance, and its dying out and final extinction. As one would expect, the fossils found in the more recently formed rocks are most like the plants living at the present day. While on the one hand the evolution of some families of plants appears to be an exceedingly slow process, for even as far back as the Ordovician there are found algae very similar in form to some of the living ones, there are on the other hand examples illustrating comparatively rapid evolution. Although the Angiosperms (plants with flowers) appear late in geological time they have already become the dominant plants of to-day. A reference to the diagram below will show that there is

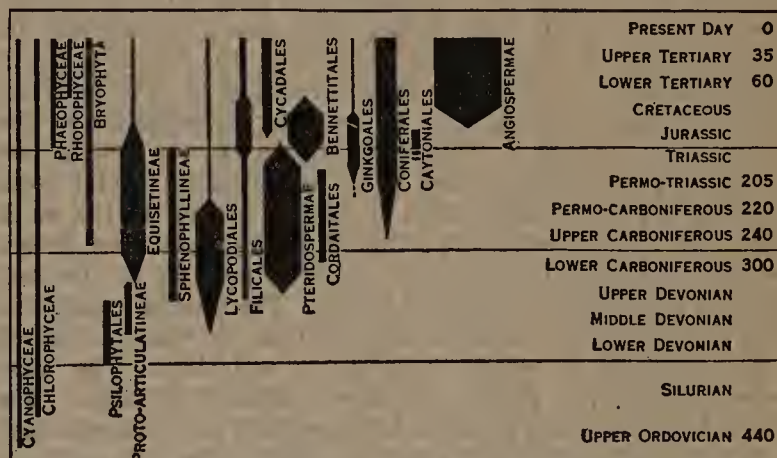


DIAGRAM REPRESENTING DURATION AND RELATIVE ABUNDANCE OF THE VARIOUS GROUPS OF PLANTS AT DIFFERENT GEOLOGICAL PERIODS, WITH THE AGES IN MILLIONS OF YEARS CALCULATED FROM RADIO-ACTIVE MINERALS

evidence that the more highly specialized groups such as the Cycadales, Bennettitales and Angiosperms have been evolved later than the comparatively simple types represented by the Algae and Bryophyta and that simplicity in structure is in general an index of primitiveness. This agrees in a general way with the theory that the more specialized and complex plants have been evolved from simpler forerunners. It must be remembered, however, that although Lycopods, Cycads and Ginkgoales are represented in the present day flora the chances are that an investigator at a future period would find no trace of them among the fossil debris of the present age since they form such a small part of the vegetation. There is no reason to believe that the present day flora of the world has attained a permanent constitution; on the contrary, it



is probably changing as rapidly, if not more rapidly, than at any part of its developmental history.

**Earliest Land Plants.**—About the close of the Silurian period and the beginning of the Devonian, land-plants appear for the first time; and all plant-fossils found in earlier rocks than these have so far proved to be Algae. It has been suggested that land-plants may have arisen from sea-weed ancestors which became established on the land and in the process of migration underwent considerable changes—a theory which is not disproved by the fossil-evidence. By the Upper Devonian period land-plants were in existence which in complexity of organization were little inferior to the plants of to-day; there were forests of tall trees, so that then the face of the earth with its mountains and forests must have appeared much as it does now. It is from fossil-plants that information has been gained of the enormous fluctuations in climate and changes in the distribution of land and sea that have succeeded one another in the history of the earth's surface. It is a striking fact that rich, perhaps tropical, floras are found in the rocks of countries now in the frigid grip of polar conditions, e.g., Greenland and Spitsbergen. In the latter country the fact that coal is found in large quantities in Devonian, Carboniferous, Jurassic and Tertiary rocks, is clear proof of vigorous vegetation in lands which at the present moment have a scanty mantle of small herbs in their more favoured valleys.

**Conditions of Fossilization.**—Before the history of the various groups of the Plant World is considered the nature of plant-fossils and the technique of palaeobotanical investigation may be briefly explained. Fossil-plants are to be found in two forms, incrustations and petrifications. The incrustations are the commonest type found and have been formed by plant-fragments becoming embedded in the mud or silt of a lake or estuary. As the sediment was changed in the course of ages into shale or sandstone rocks the plants became compressed by the vertical stress of the overlying sediment and are finally found, when the rock is split open, in the form of a thin layer of black carbonaceous matter which gives silhouettes of the plants. In many fossils this carbonaceous matter is similar to coal (*q.v.*) in composition and retains to a varying extent the outward form of the plant (Plate I., fig. 7) while the internal structure has mostly disappeared. It is possible to remove such a fossil from the rock and then the film may be translucent and some structure visible (Plate I., fig. 6). It may happen that in an incrustation the original cuticle of the plant and sometimes the spores are preserved and may be isolated by chemical treatment. The petrification is the most valuable type of fossil for investigation of the internal structure but is comparatively rare. In the petrification the entire plant fragment has been converted into solid rock, mainly by a gradual substitution of mineral matter for the water which forms such a large proportion of most plant tissues, before the plant was subjected to any considerable pressure by the sand and mud subsequently deposited over it. The mineral substances reach the plant by a process of diffusion from the water contained in the sediment in which the plant is embedded. The most perfectly preserved plants are those petrified in silica. The Middle Devonian chert found in Aberdeenshire contains embedded in its siliceous matrix fossil-plants in which every cell-wall is so clearly defined (Plate I., fig. 2) that the knowledge of their internal structure is practically complete. The beds of silica of Permian age at Autun in France have also furnished some very perfectly preserved plants. Silicified wood is common in many geological formations and a considerable number of silicified Mesozoic plants is known.

Concretionary masses known as "coal-balls" or "bullions" are found embedded in the coal of certain seams in Lancashire and Yorkshire, sometimes in such abundance that further working of the seam is unprofitable. These coal-balls consist largely of calcium and magnesium carbonates and contain well preserved plant fragments; they represent part of the vegetable matter of the seam which became petrified before the rest became compressed to form the coal. Similar concretions are found in the Belgian, Dutch, Westphalian and Silesian coal-fields. It is from the study of the plants in the coal-balls from Lancashire and Yorkshire

that Binney, Williamson and recently Scott, have been able to reveal so much about the structure of fossil-plants of the Carboniferous period. The coal-ball or other petrified mass may be cut into thin slices which are ground so thin and translucent that the cellular structure of the contained plants is made visible when viewed by transmitted light.

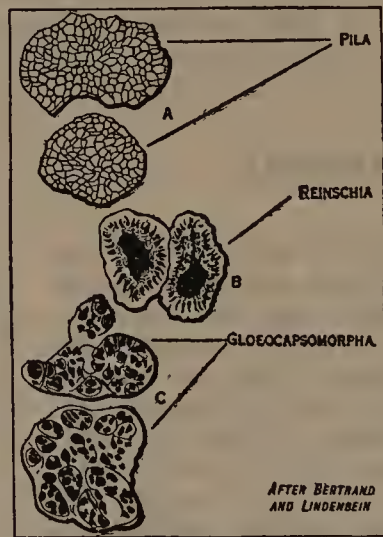
**Form Genera.**—Specimens of fossil-plants which are sufficiently complete to show the connection between the different parts of the same plant, for example between the leaves and stem or the cones and stem, are very rare. It is therefore usually convenient to constitute form-genera to include the corresponding parts of a group of closely allied species. Thus in the genus of fossil-trees *Lepidodendron* the stems are included in the form-genus *Lepidodendron*, detached leaves in *Lepidophyllum* and the cones in *Lepidostrobus*, while the root-bearing parts which are indistinguishable from those of an allied genus *Sigillaria* are grouped with those of the latter genus in the form-genus *Stigmaria*.

## PLANTS OF THE PALAEOZOIC PERIOD

In this great division of Geological time the oldest rocks which contain evidence of contemporary plant life were laid down. The various groups of plants present in the Palaeozoic will be treated in systematic order while the distribution and succession of the floras will be briefly dealt with at the end of this section. The Glossopteris or Southern type of Carboniferous and Permian flora will be considered in the section on the Mesozoic Period.

**Thallophyta.** *Algae* (Seaweeds, etc.).—As a class the Algae are difficult subjects to investigate in the form of fossils. Except in the case of a few of the groups of this large division of the plant kingdom the plant body is soft, consisting of a very large proportion of water, and therefore offering a very small amount of solid matter for the making of a fossil. In external form so many Algae are alike; they are often undifferentiated into stem and leaves, *i.e.*, thalloid, and unless there is information available about their method of reproduction external form alone is of little value in determining their systematic position. A great many supposed fossil-algae have been described and named but it can often only be said about them that the outline of the mark they

make on the rock suggests the outline of the frond of a seaweed. If none of the carbonaceous constituent of the plant is left and no cellular structure preserved such a fossil is of no scientific value. Some purely physical causes such as the flow of a small trickle of water over a mud surface can produce shapes like branching fronds and it has been shown fairly conclusively that certain marks which at one time were supposed to represent Algae in some early rocks are no more or less than the tracks of worms or some other animals in the mud which was finally consolidated to form the rock. Where organic residue is present and there is evidence that the structure is really of vegetable origin further information cannot be got



FROM (A, B) BULLETIN DE LA SOCIÉTÉ BELGE DE GÉOLOGIE, (C) BULLETIN DE LA SOCIÉTÉ BOTANIQUE DE GENÈVE

FIG. 1.—SOME ALGAL CONSTITUENTS OF COAL AND BITUMINOUS SHALES

without cellular structure as a guide as there are other plants beside algae which have a thalloid form, e.g., some Liverworts.

The *Schizophyceae* were present in all probability as early as the Cambrian. *Marpolia spissa*, one of several thalloid and filamentous types found in Middle Cambrian rocks in British Columbia shows structure which indicates that what appear to be branching filaments are really compound, consisting of several cellular filaments united in a sheath. The cells of the filaments are exceedingly small. These features are also exhibited by the living genus *Schizothrix* of the Schizophyceae. *Archaeothrix oscillatori-*



*formis* discovered by Kidston and Lang in the Middle Devonian chert of Aberdeenshire is an Alga consisting of cellular filaments which are so like those of some living Schizophyceae that there is no doubt of its systematic position in that group. *Pachytheca*, a small spherical algal colony built up of filaments of a similar type is a characteristic fossil of the Silurian and Devonian and appears to be related to the Schizophyceae.

The *Chlorophyceae* (Green Algae) are not certainly known as fossils but it seems probable that they may have existed in the Palaeozoic. A considerable deposit of a combustible material is known in Silurian rocks to the east of the Baltic. This deposit (Kuckersite) consists of a fossil-alga *Gloeocapsomorpha* (fig. 1 C). The affinities of this plant are doubtful but it may well be a green Alga. It has been shown that many bituminous shales and cannel coals are mainly formed of a deposit of small algal colonies. *Pila* and *Reinschia* (fig. 1, A and B) form the main algal constituent of many shales and coals of Carboniferous and Permian age. The building up of combustible deposits of a similar nature is taking place at the present day: a green alga, *Botryococcus coorongiana*, almost identical in the form of its cell-colonies with *Reinschia*, forms masses of tough bituminous matter on the shores of certain South Australian lagoons. While alive these algae store up oil in their cells and it is this oil which on the death of the organism permeates the whole mass and gives the bituminous properties to this "coorongite" and presumably also to the fossil deposits built up of algae with a similar cellular structure such as *Reinschia*. The existing families of the Codiaceae and Dasycladaceae are represented as far back as the Ordovician and provide us with the longest and perhaps most complete historical record of any living group of plants. In several of the genera of both families a thick calcareous deposit accumulates on the outside of the cell-wall and it is in virtue of this deposit that they have been preserved and that some are important constituents of limestones formed during various geological periods. *Dimorphosiphon*, *Palaeoporella* and *Cyclocrinus* are some of the Ordovician genera. *Dimorphosiphon* is remarkably like the living genus *Codium* but differs in having a secretion of lime on its surface.

*Charophyta* (Stoneworts).—There is evidence of the presence of plants allied to the stoneworts in the Devonian; *Palaeonitella*, from the Aberdeenshire chert, with its whorled branch segments, is very like a small *Nitella*.

*Fungi* (Moulds, etc.).—Abundant remains of fungal filaments and resting spores have been found in the Aberdeenshire chert and establish the presence of Phycomycetous fungi in the Middle Devonian. Some of the filaments have numerous septations which as Kidston and Lang have suggested may indicate the presence of higher fungi (*Eumyces*) as well. There are several records of Phycomycetes from the Carboniferous and Permian while F. E. Weiss has demonstrated the presence, in a coal-ball, of roots belonging to some gymnosperm infected with fungal hyphae. The distribution of the fungus in the tissues suggests that here is an example of the symbiotic relationship of fungus to higher plants which is known as mycorrhiza.

*Bacteria*.—A number of supposed fossil bacteria have been described from Palaeozoic rocks but they are of practically no scientific value. It is however practically certain that bacteria existed because petrified plant remains are found which show clear evidence of decay and no traces of fungi are visible.

*Thallophyta of Uncertain Systematic Position. Nematophyton*. In the Silurian and Devonian, in several parts of the world, fragments of a large plant are found the whole bulk of which was built up of loosely packed tubes, the larger running parallel to the axis while finer ones are found forming an inter-lacing system between them. In one specimen in which the outer surface is preserved there is a narrow zone where the tubes turn outwards and meet the surface at right angles. This type of construction is typically algal but the size of the fossils, some of which reach a thickness of three feet, show that they are quite unlike any living alga. In *Sporocarpion* from the Upper Devonian of America only the tips of the branches of what must have been a thalloid plant have been found. These tips are forked and rows of isolated

tetrads of spores are found embedded in the tissue in each branch. The resistant nature of the spores suggests that they may have been cutinised like those of the Pteridophyta. Cutinised spores are also found in the lower Devonian plant *Parka*, the "puddock spawn" of the Forfarshire quarrymen, which consists of small circular thalli with small rounded masses of spores embedded in them.

**Bryophyta.**—Mosses and liverworts are found in almost every type of vegetation at the present day and it is surprising that

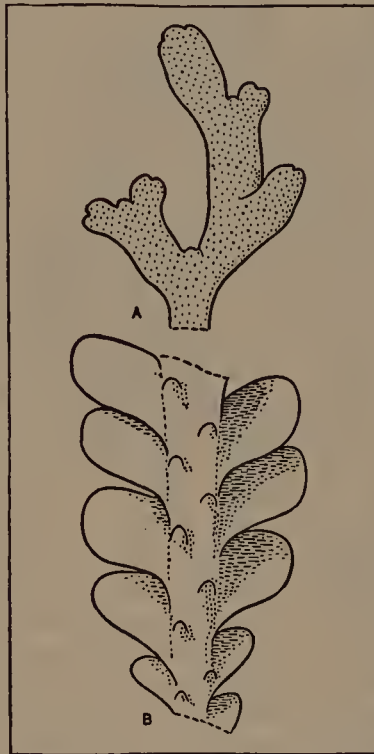


FIG. 2.—CARBONIFEROUS LIVERWORTS

A. Thallose type. B. Leafy type

they are so rare in the fossil state. On structural grounds they must be considered a relatively primitive and simple type of plant. Several fossil liverworts are known from the Upper Carboniferous of England. *Hepaticites Kidstoni* is a very small plant (fig. 2, B) with two parallel rows of leaves one on either side of a relatively stout axis and two rows of smaller scale-like leaves along the surface of the axis. In *H. Willsii* (fig. 2, A) and *H. Langii* the plant is thalloid consisting of a ribbon-shaped body which forked repeatedly. In *H. metzgerioides* a strand of conducting cells is present along the middle of the thalloid body of the plant. All these liverworts appear to be most closely related to the anacrogynous liverworts and compare very closely with some of the living ones in their vegetative structure. There is no evidence of the presence of acrogynous liverworts. Small shoots

have spirally arranged leaves preserved as incrustations. *Muscites polytrichaceus*, and a very small petrified stem, which has absorptive hairs with oblique cross walls, *M. Bertrandi*, have been found in Upper Carboniferous rocks in France, demonstrating fairly conclusively the existence of mosses at that period.

**Pteridophyta. Psilophytales.**—Among the several very incompletely known plants of the Lower Devonian, *Psilophyton princeps* may be cited as representing one of an important group of plants which have certain primitive attributes. The name was given to some specimens from Canada by Sir J. W. Dawson more than half a century ago. Owing to the discovery of large masses of silica containing petrified plants in beds of Middle Devonian age in Aberdeenshire Kidston and Lang have been able to reconstruct, almost in their entirety, some plants which are closely related to Dawson's *Psilophyton princeps*. The plants are found petrified in their position of growth and five species grouped in three genera have been distinguished which with *Psilophyton* constitute the Psilophytales. One of them, *Rhynia Gwynne-Vaughani* (fig. 3, B) a small plant with cylindrical shoots, about 8 in. in height, is remarkable for having no leaves or roots. The lower parts of the shoots were horizontal and were furnished with small tufts of absorptive hairs on the under surface; while the presence of stomata on the vertical parts bears witness to their having been aerial and green. Another species, *Rhynia major*, was a slightly larger plant but both species of *Rhynia* must have been much alike in appearance. Sporangia are found on the tips of some of the aerial branches containing numerous spores (Pl. I., fig. 2) which were produced in tetrads as in other Pteridophyta. The internal structure of the shoot is simple (Pl. I., fig. 1); a single strand of xylem (wood) in the centre surrounded by a sheath of phloem (bast) constituted the vascular cylinder or stele. The cortex is wide in relation to the vascular tissue and consists of an inner zone of thin walled cells with large intercellular air spaces and an outer zone, two or three layers deep, of large cells which are elongated at right angles to the surface. The epidermis con-



sists of a single layer of smaller, slightly thicker-walled cells and had a well developed cuticle. The stomata are infrequent and each consists of two simple guard cells surrounding a pore. Small adventitious branches are found attached to some of the shoots and as there is no vascular connection between the adventitious branch and the shoot it is probable that these branches were easily detached and served to propagate the plant vegetatively.



AFTER KIDSTON AND LANG BY COURTESY OF THE ROYAL SOCIETY OF EDINBURGH

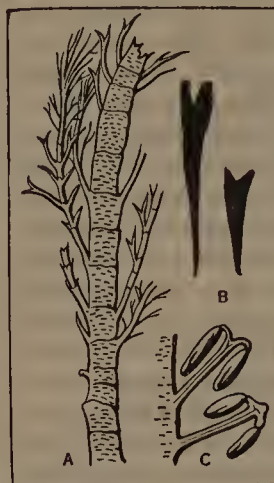
FIG. 3.—TYPES OF LANDPLANT FROM THE DEVONIAN OF SCOTLAND. A. ASTEROXYLON, B. RHYNIA

*Hornea Lignieri*, a plant of similar dimensions and habit, has tuberous swellings at the base of the shoots. The differentiation of vascular tissue, which forms a cylindrical strand in the stem, only extends for a short distance into the swollen base, whose under surface bore absorptive hairs. The sporangia differ from those of *Rhynia* in having a sterile column of tissue extending from the base up into the midst of the sporangium. This column has been compared with the columella found in the capsules of the Liverworts and Mosses. In both *Rhynia* and *Hornea* the sporangia look something like swollen branch-tips and in *Hornea* branched sporangia are known.

*Asteroxylon Mackei* (fig. 3, A) a more complex plant, had smooth horizontal stems with small root-like branches; true roots are absent just as in *Rhynia* and *Hornea*; the aerial shoots are erect and densely clothed with small scale-like leaves. The stele contains a fluted column of xylem which appears in section like a multi-rayed star. Small strands of tracheids connected with the stele pass out towards each leaf but stop short before entering the base of the leaf which had no vascular tissue. In *Thursophyton* a probably closely allied plant from the Middle Devonian the leaves are small and spine-like and vary considerably in size. These facts suggest that in plants of the small-leaved type such as the lycopods the leaves may be the homologues of spines or in other words the small leaf of the lycopod may have evolved from a small spine or emergence of the shoot by a gradual process of vascularisation, an early stage in the process being represented by the condition found in *Asteroxylon* where the vascularisation has not yet extended from the shoot into the leaf itself. The sporangia of *Asteroxylon* were borne, in all probability, on small smooth branches. Another species of *Asteroxylon* has been found in Germany which has leafless upper branches, comparing therefore with the supposed fertile branches of the Scottish plant. Nothing is known about the sexual generation of these Devonian plants. A consideration of the Psilophytales as a group suggests that they may represent, in the *Asteroxylon*-type with its small leaves, the fore-runners of the Lycopods. The branching shoot of *Rhynia* with its terminal sporangia suggests that the large megaphyllous fern frond with sporangia on its edges may have originated from such a branching shoot. The column of tissue in the sporangium of *Hornea* suggests comparison with the columella of the moss or liverwort. The living group, the Psilotales, which compare with *Rhynia* in being rootless and sometimes almost leafless but which differ considerably in the position of the sporangia on the plant, may also be related. Finally, in the absence of differentiation into stem and leaves, the plant body of *Rhynia* with its simple thalloid form calls attention to the suggestion put forward by more than one writer that land-plants are descended from algal ancestors. It has been remarked that the sporangia in the vascular plants correspond morphologically to the branches of the algal thallus which bear the reproductive organs (e.g., the stichidia in the red sea-weeds). This is interesting in view of the resemblance between sporangia and branch tips already referred to in *Hornea* and to the structure of the fertile branches in *Sporocarpon* the Upper Devonian thallopiphyte in which the tips bear isolated tetrads of spores. There

was clearly in Devonian times a group of plants in existence in which there was a combination of thallopiphyte and pteridophyte characters and, as Kidston and Lang point out, "the facts are . . . consistent with the Rhyniaceae finding their place near the beginning of a current of change from an Alga-like type of plant to the type of the simpler Vascular Cryptogams."

*Articulatales*.—This large group of the Pteridophyta includes the Proto-articulateneae, Sphenophyllineae, and the Equisetineae.



FROM KRAÜSEL AND WEYLAND, "DEVONFLORA" (SENCKENBERGISCHE NATURFORSCHENDE GESELLSCHAFT)

FIG. 4.—ARTICULATE PLANT OF MIDDLE DEVONIAN AGE (CALAMOPHYTON PRIMAEVUM) A. Small branch. B. Leaves. C. Two sporangiophores; each with two sporangia

those of the whorl below and are usually in multiples of three. This arrangement is related to the structure of the stele which is triangular in section and has a central column of xylem; at the nodes two vascular strands pass out from each corner to supply the leaves. The stems and roots have a considerable amount of secondary vascular tissue. While not much variation is shown in the vegetative parts of the known species of *Sphenophyllum* there is considerable variety in their cones. In *Sphenophyllum Dawsoni* the cones are several inches long and at least half an inch thick. They are built up of whorls

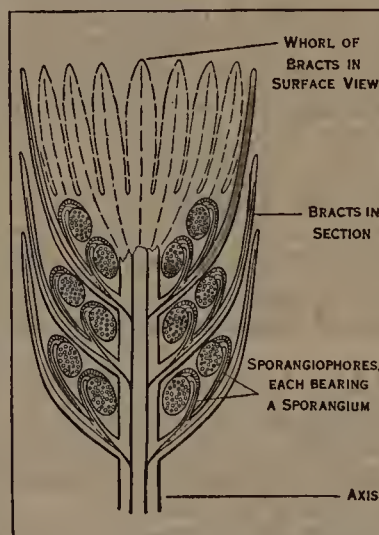


FIG. 5.—SPHENOPHYLLUM DAWSONI Diagram showing longitudinal section of the cone

bore two sporangia. This arrangement suggests that bracts and sporangiophores may be equivalent structures and that the cone of *Sphenophyllum* may be regarded as being built up of a series of bi-lobed leaves, the ventral lobes being fertile while the dorsal assumed the form of subtending bracts. In *S. fertile* this theory receives support as dorsal and ventral lobes reveal their equivalence by both being fertile. In other species there are no distinct terminal cones; nodes with fertile leaves alternate with nodes

The first is represented in the Middle Devonian of Germany by *Calamophyton primaevum* (fig. 4) a plant recently described by Kraüsel and Weyland. The stems are jointed and have small bifid leaves attached at the nodes. The sporangia are borne in pairs on modified leaves which compare closely therefore with the sporangiophores of the Equisetineae. *Hynia* of the same age has small deeply cleft leaves and in vegetative features resemble the Sphenophyllineae. The fertile leaves are forked and two or three sporangia are borne on the ends of each division.

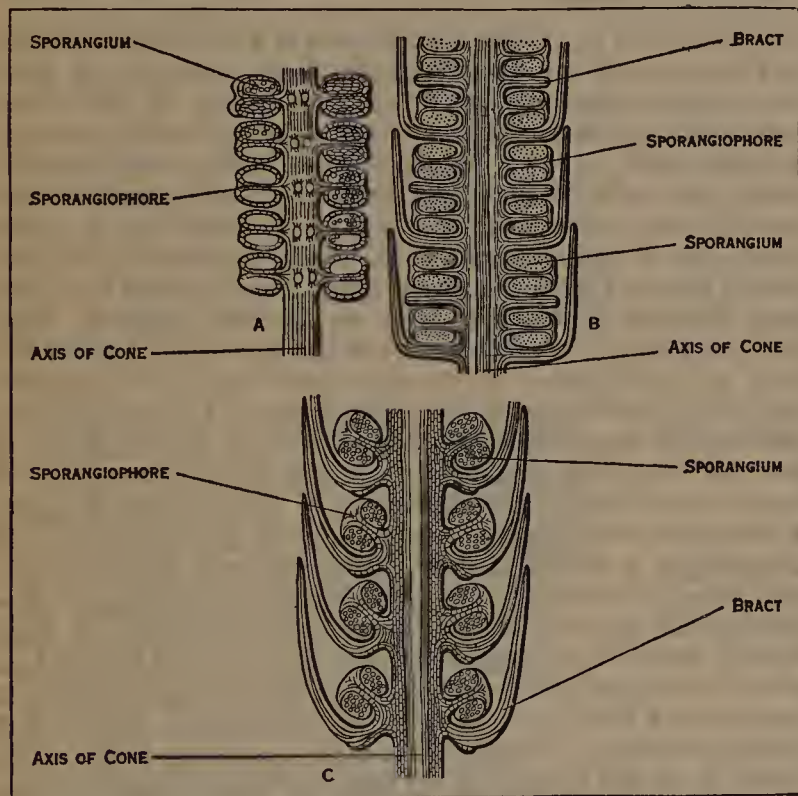
*Sphenophyllineae*.—*Sphenophyllum*, a genus common in the Carboniferous, ranges from the Upper Devonian to the Triassic. The plant grew in the form of a slender shrub which may have supported its branches by scrambling over other plants. The stems are jointed with whorls of small wedge-shaped leaves, which are often deeply dissected (Pl. I., fig. 8). The leaves of one whorl lie immediately above

those of the whorl below and are usually in multiples of three. This arrangement is related to the structure of the stele which is triangular in section and has a central column of xylem; at the nodes two vascular strands pass out from each corner to supply the leaves. The stems and roots have a considerable amount of secondary vascular tissue. While not much variation is shown in the vegetative parts of the known species of *Sphenophyllum* there is considerable variety in their cones. In *Sphenophyllum Dawsoni* the cones are several inches long and at least half an inch thick. They are built up of whorls of leaf-like bracts and those of each whorl are coherent laterally for half their length from the base so that each whorl forms a cup (fig. 5). The whorls of bracts overlap so that the cone is covered on the outside by their overlapping tips. The sporangia are twice as numerous as the bracts and are attached by narrow stalks (sporangiophores) to the upper surface of the sheath of bracts close to the axis of the cone. The sporangiophores are not all of the same length so that the sporangia had the appearance of being arranged in more than one whorl in each cup. In *Bowmanites* a cone belonging to some closely related plant, the sporangiophores had a bract-like expansion at the end and each



bearing sterile leaves. This hypothetical bi-lobed leaf may also be distinguished in *Cheirostrobis*, a very complicated cone of Lower Carboniferous age. Here the leaf is divided into three dorsal sterile and three ventral fertile segments. Each fertile segment bears four sporangia and in construction is exceedingly like the sporangiophore of the Equisetineae and it is possible that *Cheirostrobis* is a representative of the stock from which the Sphenophyllineae and Equisetineae have both sprung.

*Equisetineae*.—The fossil Equisetineae were at their zenith in Carboniferous times; in place of the small, herbaceous *Equisetum* (horse-tail) of to-day there were gigantic trees some with a girth of three metres and a height of 60 metres forming a conspicuous feature in some aspects of the vegetation. *Calamites* the best known genus had the same habit as the horse-tail with jointed stem and small leaves but differed in its much greater size. The internal structure of the stems, roots and leaves, is in many respects like that of *Equisetum* only there is secondary thickening in the stems and roots. The leaves, usually small, linear or lance-shaped, are often united near the base to form a sheath round the stem. Like *Equisetum* the stems are hollow with a large central cavity. Casts of these cavities in sandstone are frequently found showing longitudinal grooves representing the courses of the primary woody strands which projected into the pith cavity. There is a constriction on the cast at each node and the grooves of one internode alternate with those on the internode above and below. Two main types of calamite-foliage are known: *Asterophyllites* and *Annularia*; in the former the leaves are long and awl-shaped and quite separate. In *Annularia* the leaves are usually more paddle-shaped terminating in a small sharp point. The single vein which passes out into this point had, in some species, a swelling near the tip of the leaf suggesting the presence of a water gland. In another type of *Annularia* the margins of the leaf were inrolled and bore a fringe of hairs which probably sheltered the stomatal surface of the leaf. The cones exhibit a considerable range in form, indicating that several families and genera may be



(A AND B) FROM RENAULT, "BASSIN HOUILLE ET PERMIEN D'AUTIEN ET D'ERPINAC," BY COURTESY OF THE MINISTER OF PUBLIC WORKS (FRANCE)

FIG. 6.—EQUISETALEAN CONES, SHOWING LONGITUDINAL SECTIONS OF (A) ARCHAEOCALAMITES, (B) PALAEOSTACHYA, (C) CALAMOSTACHYS

included in *Calamites*. In *Calamostachys* the cones were terminal on the branches and the axis of the cone bore whorls of peltate sporangiophores similar to those of *Equisetum* but alternating with whorls of sterile bracts (fig. 6, C). The sporangiophores are in superposed whorls while the bracts of one whorl alternate with those above and below. Each sporangiophore bears four sporangia in which the spores are found sometimes arranged in tetrads. In some species the spores in the cone are all of the same size but

other species are heterosporous some sporangia having large numbers of small spores while others in the same cone had a smaller number of large spores. In *Palaeostachya* (fig. 6, B) the sporangiophores unlike those of *Calamostachys* are attached in the axile of the bracts which subtend them. In *Archaeocalamites*, a characteristically Lower Carboniferous plant, the leaves are long and may be twice forked while the vascular strands of the inter-

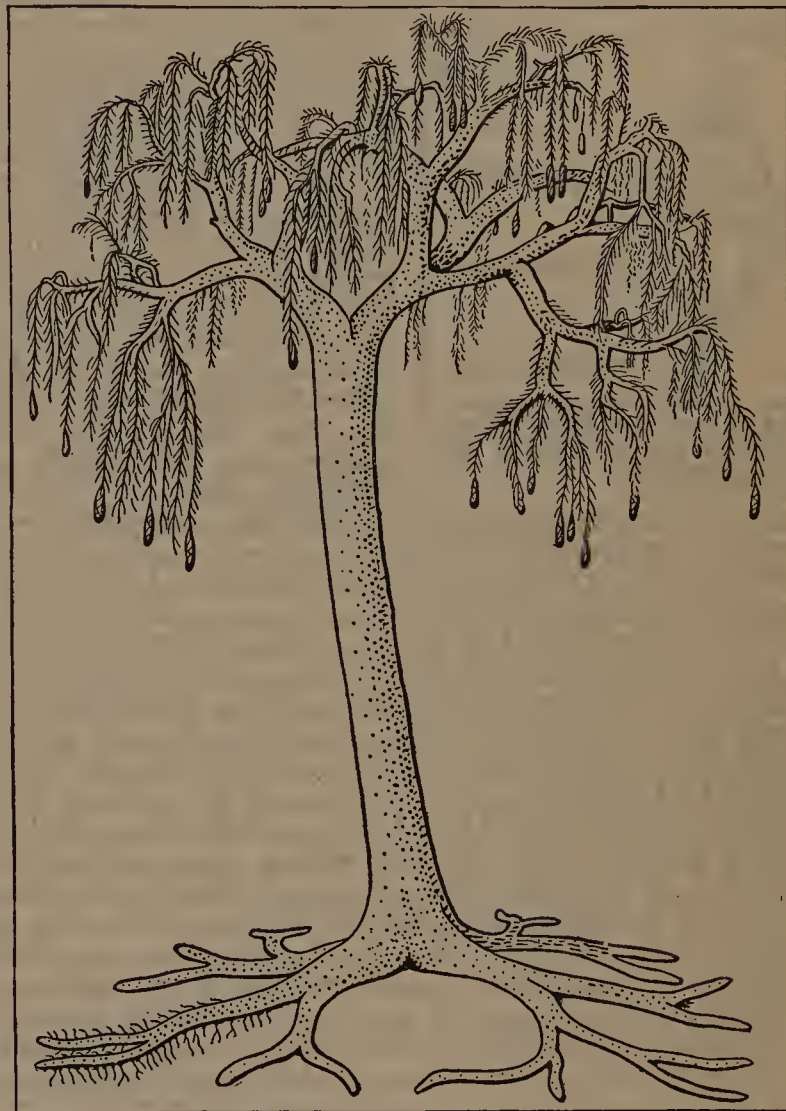


FIG. 7.—RECONSTRUCTION OF A LEPIDODENDRON, SHOWING THE STIMARIAN BASE, TRUNK, LEAVES AND CONES

nodes pass straight through and do not alternate at the nodes. The cones (fig. 6, A) are very like those of *Equisetum* but are long and constricted at intervals where forked leaves were attached so that they resemble a branch in which the internodes are covered with sporangiophores. Although the presence of heterospory and secondary thickening are probably stages in the direction of a gymnospermous type the Equisetineae must be considered as essentially Pteridophyta.

*Lycopodiales*. (Club-Moss allies.)—The lycopods are typically small-leaved plants. There are three living genera: *Selaginella*, *Isöetes* and *Lycopodium*, interesting in view of their relation to the Palaeozoic members of the group: the first two are ligulate and the second has secondary thickening in its rootstock in these respects comparing with the majority of the fossils. The living forms must be regarded as the remnant of a once important group; they are all herbs, whereas the fossils were almost all trees.

(a) Ligulateae. *Lepidodendron* (fig. 7) which may be taken as the type of the group is of extended geological range; while *Protolopodendron*, a very doubtfully related plant, is of Middle Devonian age *Lepidodendron* itself ranges from the Upper Devonian to the Permian. The trunk reached a height of over 114 ft. while above that the crown of forking branches rose for a further 20 ft. The lance-shaped leaves are usually from one to four inches in length but sometimes reached the length of a yard; they were shed when the part of the plant bearing them reached a certain age leaving a scar on the persistent leaf-base (fig. 8 and



Pl. I. fig. 7). The ligule, a small secretory scale, is situated in a pit on the leaf-base just above the point of attachment of the leaf. The leaf-bases are diamond-shaped in outline and are very regularly arranged on the surface of the stem. The leaves have a single median vein and the ventilating tissue of the leaf was connected with that of the stem by two strips of a similar tissue termed parichnos which have left the two small marks one on each side of the vascular strand on the leaf-scar (fig. 8). There were

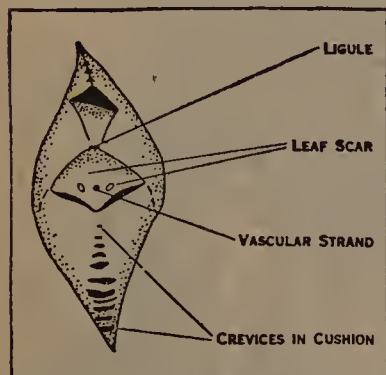
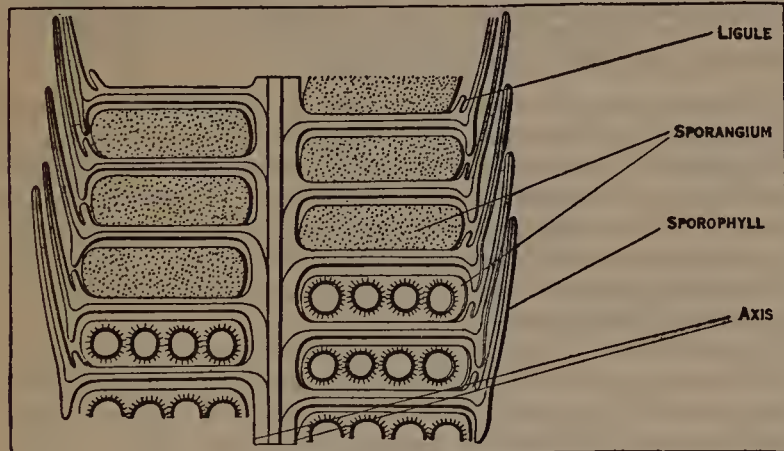


FIG. 8.—A LEAF-CUSHION FROM THE SURFACE OF A TRUNK OF A LEPIDODENDRON

deciduous side branches arranged in two vertical rows on each side of the trunk or main branches: when these became detached they left a characteristic scar. In other species there were numerous vertical rows of these deciduous branches and while it is possible that these branches may have borne the cones in yet other species the cones are known to have been placed on the ends of the ordinary foliage twigs (fig. 7). The stems and branches were traversed by a cylindrical column of primary xylem, in some species solid, but in others with a parenchymatous core. The protoxylems are situated on the outer surface of this column and from them the small vascular strands to the leaves passed out through the external tissues. In most species secondary wood was formed round the primary. External to the wood was a tissue corresponding to the phloem surrounded by the inner and outer cortex, the former a lacunar, ventilating tissue, while the latter had a cambial zone near its outer limit which gave rise to corky tissue. A thin layer of the cortex outside the corky tissue afforded a foundation for the attachment of the persistent leaf-bases and became fissured later by the expansion due to the secondary growth within. The cones were in general construction like those of *Selaginella* only much larger and as in the living genus each sporophyll bore a ligule on its upper surface close to the abaxial face of the sporangium. In *Lepidostrobus*, cones which belong to various species of *Lepidodendron*, each sporophyll consists of a stalk bearing on its upper surface a radially elongated sporangium with the ligule placed in a pit just beyond. The stalk terminated in an upturned blade. Some cones are heterosporous



FROM SCOTT, "STUDIES IN FOSSIL BOTANY" (A. & C. BLACK, LTD.)

FIG. 9.—LEPIDODENDRON, SECTION OF HETEROSPOROUS CONE

the upper sporophylls bearing micro-sporangia, while those at the base of the cone bear mega-sporangia (fig. 9).

Each megasporangium contained 8-16 megaspores. Other spores are known which bear only microsporangia or only megasporangia. It is also possible that such species bore the two kinds of cones on separate trees. Megaspores have been found with the prothallus and archegonia preserved; their reproduction must have been similar to that of *Selaginella* and it is probable that the spermatozoids which fertilised the ova in the archegonia were liberated from microspores which became entangled in the spinous processes found on the outsides of the megaspores. The chances of megaspores and microspores becoming associated in this way

were largely augmented by the enormous number of microspores produced in each microsporangium. Some coals of Carboniferous age consist very largely of compressed Lycopod spores. In *Lepidocarpon* (fig. 10, B), another type of cone, only one megaspore is present in the mature sporangium and an integument, formed from an outgrowth from the sides of the sporophyll-stalk invested the sporangium except for a narrow opening along the top. In

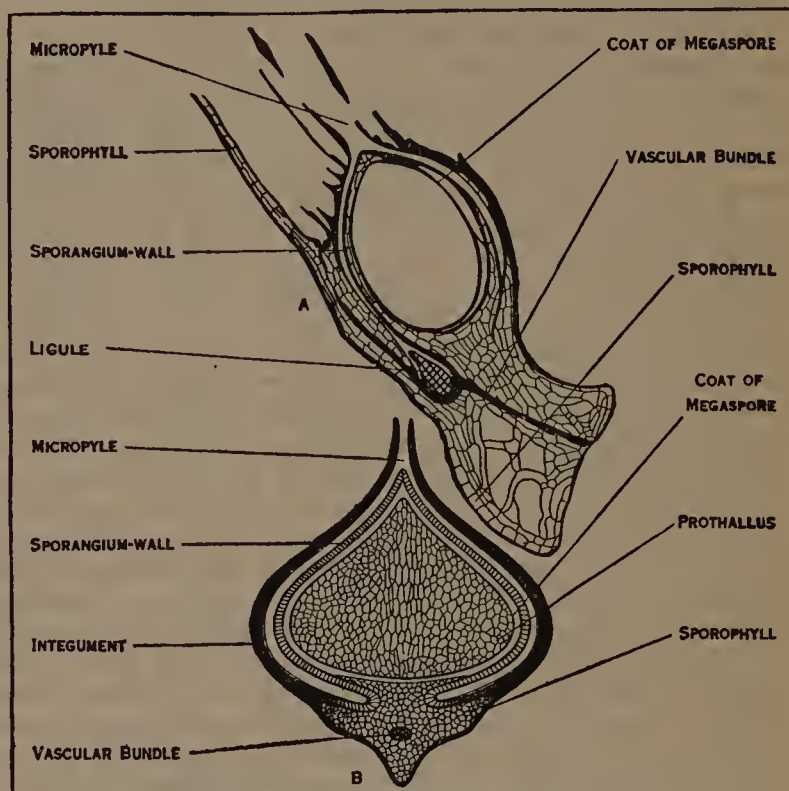


FIG. 10.—SEED-LIKE ORGANS OF SOME FOSSIL LYCOPDS

A. *Miadnesia*, longitudinal section of sporophyll. B. *Lepidocarpon*, transverse section of sporophyll

*Miadnesia* (fig. 10, A), the fructification of a herbaceous Lycopod of Carboniferous age, the integument is prolonged in the form of a sheath beyond the top of the sporangium. A fairly close comparison may be made between these two fossils and true seeds; in both fossils however, the sporophyll broke away from the parent plant with the sporangium before fertilisation took place or possibly even before microspores were deposited on it, unlike a true seed in which an embryo is usually developed before the seed is liberated from the parent plant. Among other Carboniferous lycopods *Sigillaria* occupies an important position. *Sigillaria* had a large trunk with persistent leaf bases placed either like those in *Lepidodendron* or else in vertical rows. It is probable that many *Sigillariae* were unbranched except for small, lateral, cone-bearing twigs and the tall trunks with the tufts of leaves at the tops must have presented a peculiar appearance. *Sigillaria* was heterosporous and the distribution of the two kinds of spores in the cones was probably the same as in *Lepidodendron*. In *Mazocarpon*, a sigillarian cone, the sporophylls were curiously constructed; the wall of the sporangium had a curved plate projecting from its distal end and there is no integument. A large mass of sterile tissue is present inside, and attached to, the base of the sporangium and megaspores up to the number of eight were arranged in a single layer between this sterile tissue and the wall of the sporangium. Vascular tissue is present in the centre of the sterile tissue and it connects up with the vascular strand in the sporophyll. The megaspores are concave on the side next to the sterile tissue and archegonia are present in the prothallus in each spore opposite to the place at which the spore broke open. The megaspores when dispersed broke away part of the overlying sporangium wall. *Lepidodendron* and *Sigillaria* are sometimes found attached to their root bearing parts which receive the name *Stigmara*. The base of each *Lepidodendron* or *Sigillaria* consisted of four main downwardly directed branches which spread out and forked equally and repeatedly (fig. 7). These branching systems are often found penetrating the barren sandstone or shale underneath the seams of coal and offer certain evidence that the coal has



been formed in the actual place of growth of the trees from whose remains it has been formed. The surfaces of these underground branches are covered with roots which penetrated the surrounding soil. The morphology of these root-bearing structures is not yet fully elucidated; internally they are constructed more like stems than roots and the true roots which are attached to them are only very slightly endogenous. The whole branching, root-bearing system may be closely compared with the root stock of the living *Isoetes* in which there is a peculiar type of secondary thickening and which bears roots very similar in structure to those of *Stigmara*.

(b) *Eligulatae*. This group of lycopods of which *Lycopodium* is the type are not so well represented as fossils; *Spencerites*, of Carboniferous age is the only certain eligulate Lycopod known in the Palaeozoic but it is possible that *Cyclostigma*, a Devonian genus, is eligulate, for no one has yet been able to show that a ligule is present, although poor preservation might account for that.

*Filicales* (Ferns).—One of the striking features of the assemblage of plants found in the Carboniferous rocks is the frequency of fragments of fern-like plants. Up to the end of the 19th century these were all considered to be true ferns; since then, however, evidence has been accumulating to show that many of them belong to a higher group of plants and our present knowledge of these fossils indicates that the majority of these fernlike fronds belong to an extinct group, the pteridosperms, plants which produced seeds and which cannot therefore be classed with the ferns. In addition to seeds the pteridosperms had microsporangia which contained microspores the equivalents to the pollen grains in the flowering plants. These microsporangia bearing fronds, unless their relation to the rest of the plant is established may easily be taken for fertile fern-fronds. No known pteridosperms had microsporangia bearing the specialised group or band of cells called the annulus which is part of the dehiscence mechanism of most fern sporangia; so that fronds found with annulate sporangia are almost certainly fronds of ferns. On the other hand fertile fronds with ex-annulate sporangia are known which are also certainly ferns but here it may be due to the difficulty of detecting the annulus where the plant is preserved in the form of an incrustation and the sporangia are very small. [The best known Palaeozoic ferns are preserved in the form of petrifications. Unlike the Equisetales and Lycopodiales the formation of secondary tissues was as of rare occurrence in fossil ferns as among the living and no certain examples of heterosporous ferns are known from the Palaeozoic.] The Botryopteridaceae fall into two groups: (a) *Zygopterideae*. This family contains over a dozen genera and one of them, *Asteropteris*, was found in Upper Devonian rocks in the State of New York while *Ankyropteris*, the best known genus, is represented by both Carboniferous and Permian species. *Ankyropteris Grayi* from the Lower Coal Measures of England had stems about 2cm. in diameter and of considerable length; in fact it was probably a climber. Large fronds were attached at fairly wide intervals and their petioles or stalks must have nearly equalled the stem in thickness. They were arranged in spiral series on the stem and a short cylindrical branch was present in the

axil of each leaf. It is possible that the axillary branch is just the smaller of the two branches of a forking of the stem effected close above the point of attachment of a leaf. The section of the coal-ball shown in Plate I., fig. 4, contains a stem cut transversely. The centre of the stele (vascular cylinder) appears as a small dark narrow-rayed star which consists of a mixture of parenchymatous tissue and tracheids; while surrounding this are the large tracheids of the periphall xylem whose outer limit retains the star-shaped outline. The annular space surrounding the xylem was produced

by the decay of the phloem and the wide zone of tissue occupying the greater part of the section is the cortex. The vascular structure of the leaf-stalk is peculiar, the xylem is in the form of a doubly grooved strand which appears like a double anchor in section (hence the name of the genus). The leaflets were given off alternately on each side of the petiole. In some zygopterids these leaflets were forked at their bases so that the petiole apparently bears four rows of leaflets and has a bushy habit. The

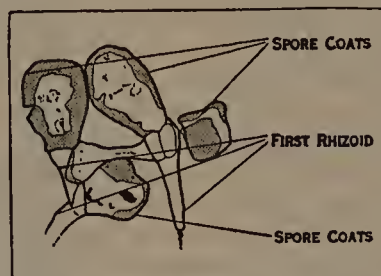


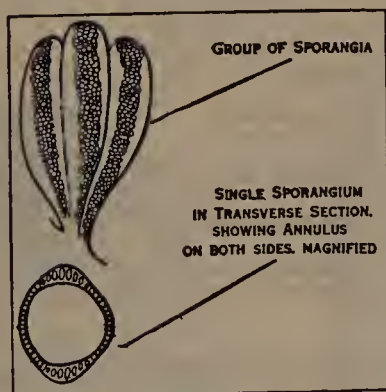
FIG. 12.—GERMINATING SPORES OF STAUROPTERIS (MAGNIFIED)

sporangia in some of the genera e.g., *Etapteris* (fig. 11) have a multiseriate annulus and are comparatively large; they were grouped in small bunches on the smaller divisions of the frond. In *Stauropteris* the stalk or rachis of the frond had four distinct rows of secondary stalks or rachises and each of these bore four rows of tertiary rachises. All the rachises are cylindrical and were presumably green as they have well developed photo-synthetic-tissue. Each frond thus consisted of a bush of small green twig-like divisions. The sporangia of *Stauropteris* had no annulus but germinating spores have been found (fig. 12) and the preliminary stages in prothallus formation is so essentially fern-like that there is no doubt that *Stauropteris* is a fern and not the pollen bearing part of a Pteridosperm, for pollen grains would behave differently on germination.

(b) *Botryopterideae*.—*Botryopteris cylindrica* has a long thin stem 2–5cm. in diameter bearing leaves at wide intervals and branching dichotomously but other plants belonging to the same family show considerable differences in habit. There is a simple stele consisting of a solid strand of tracheids with the smaller and first differentiated elements in the centre. The petiole is at its base very like the stem in structure. The sporangia differed from those of the *Zygopterideae* in being small and pear-shaped with a multiseriate annulus on one side only. The other members of the group have a more complex structure. The similarity in structure between the petiole and the stem of *Botryopteris cylindrica* is a primitive character and fits in with the suggestion that the large type of leaf or frond is derived from a subordinated lateral branch of the shoot. The Botryopterideae as a group show several points of comparison with the living Osmundaceae, representatives of which family are found in the Permian. It is also possible that the Ophioglossaceae have descended from the same stock.

*Osmundaceae*.—Petrified stems from the Permian are known which give satisfactory proof of the existence of plants closely agreeing in many anatomical details with *Osmunda* (royal fern). In *Thamnopteris* the woody cylinder was solid but the central part was like that in the *Zygopterideae* made up of parenchyma and small tracheids. There is evidence to be drawn from closely related fossils that the type of stele found in *Osmunda* has been derived in the course of descent from a solid stele such as that found in *Botryopteris*, *Zygopteris* and *Thamnopteris* suggesting intermediate steps in the process. Like *Osmunda* these Permian fore-runners had short stems with densely crowded fronds and adventitious roots. Fructifications of Palaeozoic Osmundaceae have not yet been recognized with certainty but *Discopteris*, an Upper Carboniferous form, has perhaps some claim to recognition.

*Marattiaceae*.—Petrified stems have been found which in structure are so very like those of the Marattiaceae that many botanists are inclined to regard them as proof of the existence of that group in the Palaeozoic. *Psaronius*, a form-genus of tree-ferns ranges from the base of the Upper Carboniferous upwards and is quite common in the Permian. The stem has a complex vascular system, a polycyclic dictyostele, except in *Psaronius Renaultii*, the Carboniferous species which has a colenostele. In these respects a close comparison is possible with the living Marattiaceae. In some species of *Psaronius* the fronds were attached alternately on opposite sides of the tree so that there were two vertical rows. In others there were several vertical series and as many as four fronds might be attached at the same



FROM ZEILLER, "BASSIN HOUILLES DE VALENCIENNES"

FIG. 11.—ETAPTERIS PINNATA



height from the ground. There was no secondary thickening but the stems were buttressed by a considerable development of adventitious roots forming a fibrous investment round them and giving them considerable rigidity. Several types of fertile fronds of Carboniferous plants are known which, though probably for the most part Pteridosperms, are fern-like and bear microsporangia grouped in synangia somewhat like those of living Marattiaceae ferns. *Asterotheca* has large multipinnate fronds which in the sterile condition would be grouped in the form-genus *Pecopteris*. The sporangia are united in synangia (fig. 13 A and A') which are attached to small protuberances on the surface of the frond. In *Scolecopteris* the synangium has a short stalk with a central vascular strand. In the closely allied *Acitheca* the synangium has no stalk but a vascular strand is present in the central column of tissue round which the sporangia are joined and each sporangium terminates in a sharp bristle. In *Ptychocarpus* the sporangia are more intimately united and not so pointed. *Danaeites* an Upper Carboniferous type has long linear synangia, very like those of the living *Danaea*, with two rows of about 10 closely packed sporangia each of which opened by a terminal pore. In view of the fact

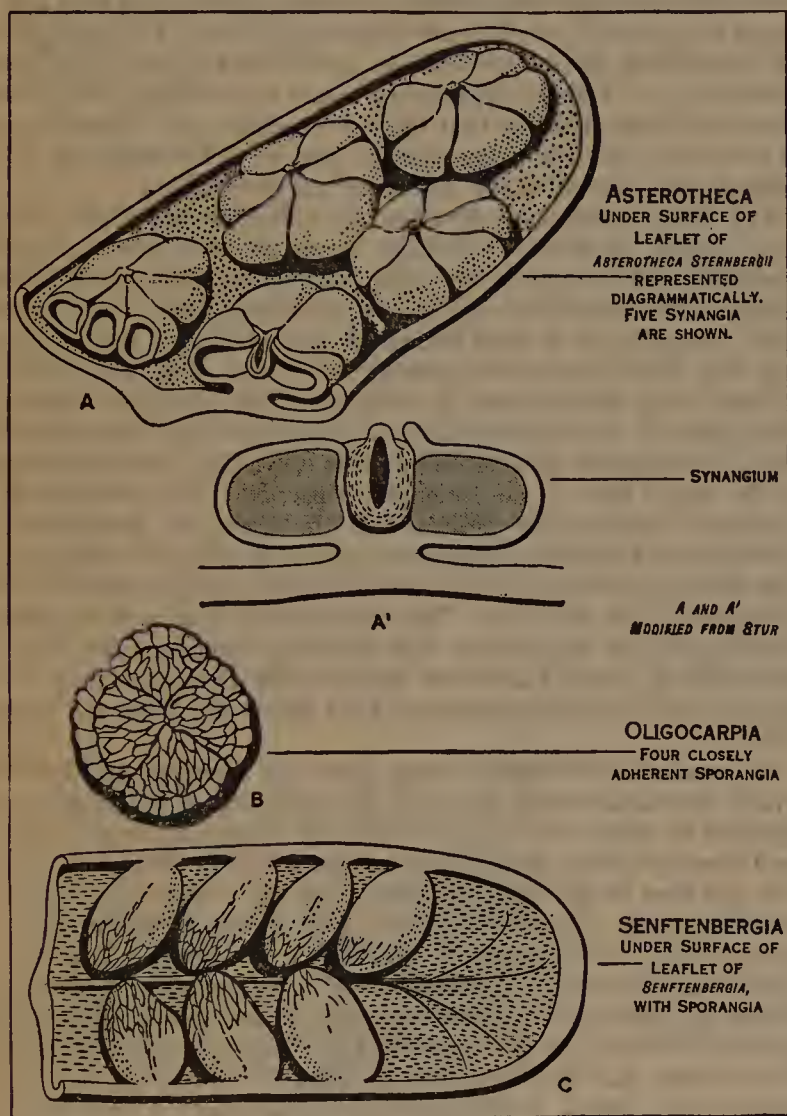


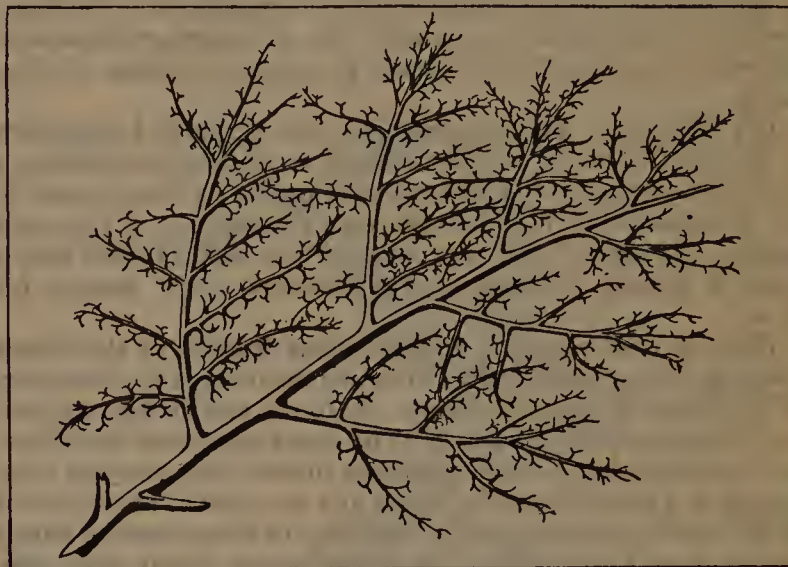
FIG. 13.—SPORANGIA OF SOME CARBONIFEROUS FERNS AND PTERIDOSPERMS

that some fructifications, known to belong to Pteridosperms, were in the form of synangia it is as yet uncertain whether most of the plants included in *Asterotheca*, *Scolecopteris*, etc., are ferns or pteridosperms. The evidence for the existence of Marattiaceae in the Palaeozoic rests primarily on the Marattiaceous structure of the *Psaronius* stems.

**Schizaeaceae.** The sporangia of *Senftenbergia* (fig. 13, C), an Upper Carboniferous genus, like those of the living *Schizaea* have an apical group of thick-walled cells constituting an annulus. An apparently closely allied genus *Klukia* of Jurassic age would seem to form a link between *Senftenbergia* and *Schizaea* as regards the sporangial structure.

**Gleicheniaceae.** The evidence for the presence of Gleicheniaceae

in the Palaeozoic is also slight; *Oligocarpia*, an Upper Carboniferous fern, shows in the form and grouping of sporangia close resemblance to the living *Gleichenia*. The fact that the annulus is sometimes formed of more than one series of cells led Kidston to doubt its relationship to the Gleicheniaceae; but sporangia are sometimes found with more than one series in *Gleichenia* so that this objection is not completely justified. *Chansitheca* from the

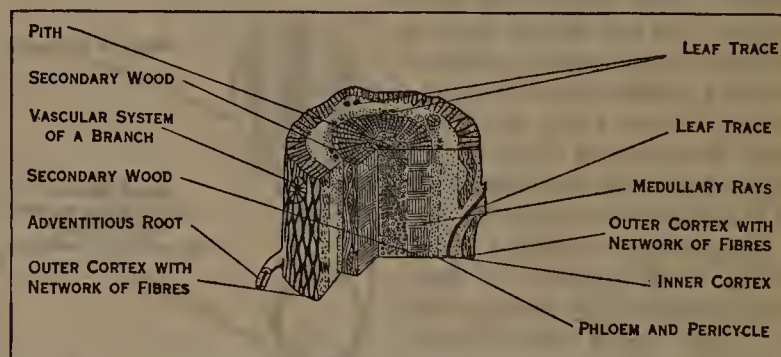


FROM KRAUSEL UND WEYLAND, "DEVONFLORA" (SENCKENBERGISCHE NATURFORSCHENDE GESELLSCHAFT)

FIG. 14.—ANEUROPHYTON, ONE OF THE MOST ANCIENT FRONDS KNOWN, FROM THE MIDDLE DEVONIAN OF GERMANY

Chansi district in China also of Upper Carboniferous age has as many as 20 sporangia in each group or sorus. It is not until the early part of the Mesozoic that undoubted Gleicheniaceae are encountered.

**Pteridosperms.**—A considerable number of fossils are known which have in their vegetative structure such similarity to the Ferns and indeed may well have evolved from an ancestral group of Ferns by developing in the course of their history an advanced type of heterospory in which seeds (*i.e.*, integumented megasporangia) were produced and pollination or the provision of pollen grains (microspores) to the seed took place before the seed was liberated from the parent plant. No Pteridosperms have survived to the present day, they were apparently extinct by the middle of the Jurassic period. *Eospermatopteris*, a plant rather like a tree-fern in habit with large fronds consisting of finely divided rachises and practically no lamina, has been found in the Upper Devonian rocks of New York with seed-like bodies attached to its fronds. *Hostimella racemosa* a Middle Devonian fossil from



AFTER W. C. WILLIAMSON, IN "TRANSACTIONS OF THE ROYAL SOCIETY"

FIG. 15.—DIAGRAMMATIC RECONSTRUCTION OF THE STEM OF LYGINOPTERIS

Scotland consisting of branching linear stalks bore, on short lateral branches, oval-bodies which though certainly sporangia might conceivably be seeds while fronds called *Aneurophyton* (fig. 14) have been found in the Middle Devonian of Germany closely resembling the fronds of *Eospermatopteris*; so that there is a certain amount of circumstantial evidence for the presence of Pteridosperms as early as the Middle Devonian. In the Lower Carboniferous Pteridosperms form an important constituent of the vegetation and maintain that position right through the Carboniferous, Permian and Triassic; in the Jurassic they disappear. The





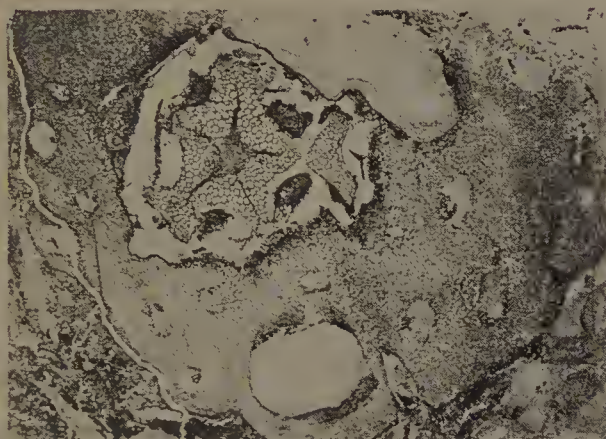
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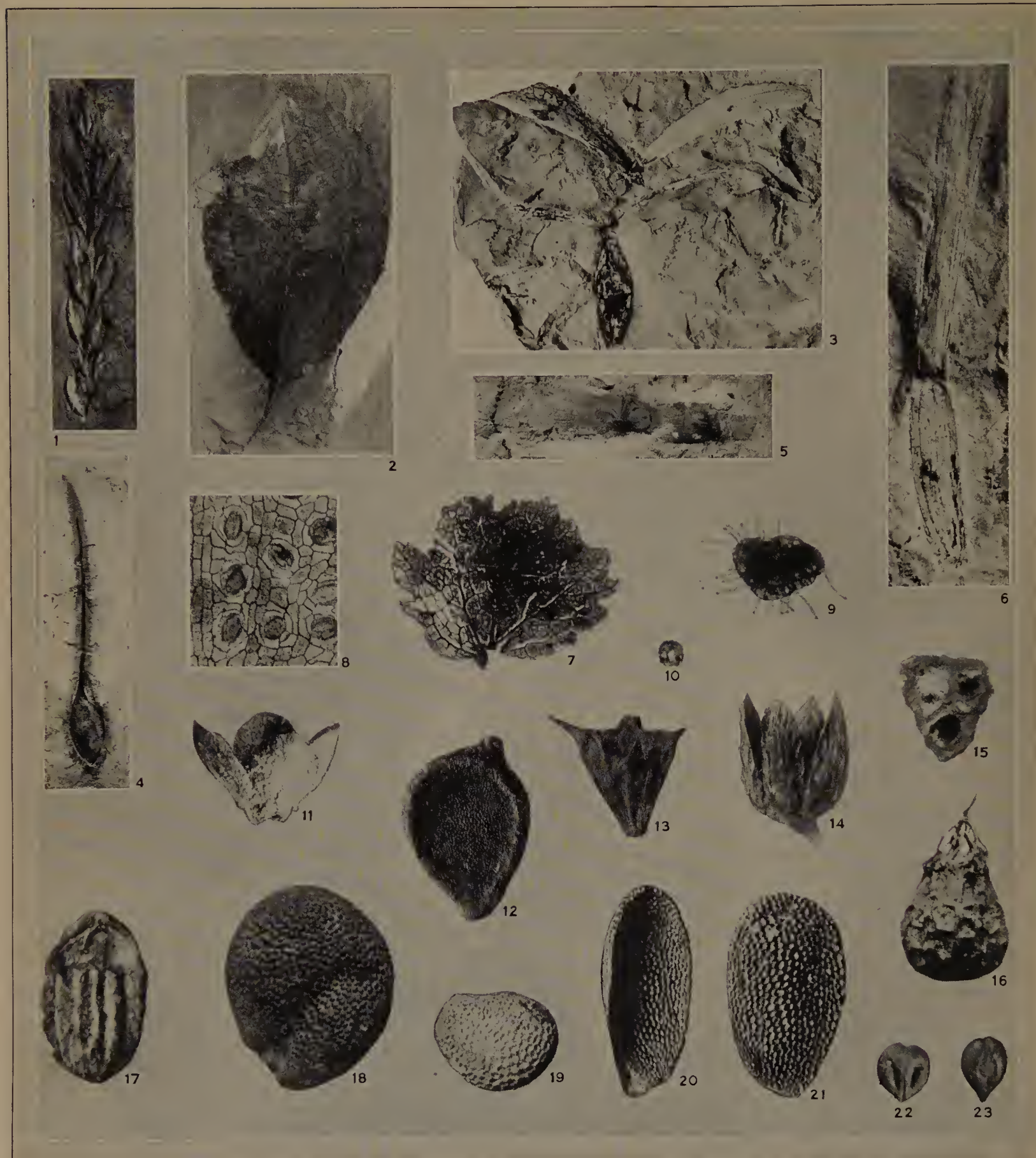
BY COURTESY OF (1, 2) THE ROYAL SOCIETY OF EDINBURGH, (9) PREUSSISCHE GEOLOGISCHE LANDESANSTALT, FROM WEISS, "STEINKOHLEN-CALMARIEN"; FROM (8) PHOTOGRAPH BY HEMINGWAY, FROM SCOTT, "STUDIES IN FOSSIL BOTANY" (A. AND C. BLACK, LTD.); (4) D. H. SCOTT, "ON A PALAEOZOIC FERN," IN ANNALS OF BOTANY (CLARENDON PRESS)

#### PLANT FOSSILS OF THE PALAEOZOIC PERIOD

1. *Rhynia major*, cross section of stem (after Kidston & Lang). 2. *Rhynia major*, sporangium in longitudinal section (after Kidston & Lang). 3. *Lyginopteris Oldhamia*, Frond showing the forking of the main leaf stalk (after Potonié). 4. *Ankyropteris Grayi*, cross section of stem

(after D. H. Scott). 5. *Sphenopteris obtusiloba* (after Walton). 6. *Renaultia gracilis* (after Walton). 7. *Lepidodendron* sp. 8. *Sphenophyllum saxifragaefolium*. 9. *Paracalamostachys polystachya*, branch with leaves and cones (after Weiss)





BY COURTESY OF (7, 11, 18, 19, 22, 23) E. M. REID AND MISS M. E. J. CHANDLER, (1-6, 6-10) THE TRUSTEES OF THE BRITISH MUSEUM OF NATURAL HISTORY, FROM REID AND CHANDLER "CATALOGUE OF CAINOZOIC PLANTS," (12-17, 20, 21) THE INSTITUTE OF GEOLOGICAL EXPLORATION OF THE NETHERLANDS FROM E. M. REID "THE PLIOCENE FLORA OF THE DUTCH-PRUSSIAN BORDER"

**FOSSIL TERTIARY AND QUATERNARY PLANTS TO ILLUSTRATE MODES OF PRESERVATION AND VARIETY OF ORGANS. FIGURES 1-6, IMPRESSIONS ON ROCK. FIGURES 7-23, ORGANS FREED FROM MATRIX**

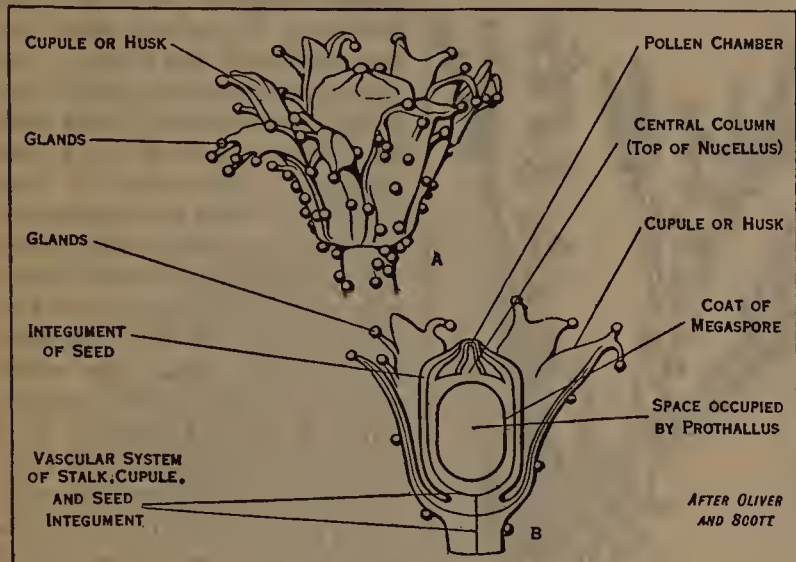
Note: The name of the series in which the fossil occurs, Bembridge, etc., follows the name and description of the plant: O. signifies Oligocene; P., Pliocene; and E., Eocene; x 2, etc., indicates approximate magnification in diameters

1. *Araucarites gurnardi*, twig, Bembridge, O. x 2. 2. *Zizyphus paradisiacus* var. *paradoxus* leaf, Bembridge, O. x 2. 3. *Abelia trialata*, fruits showing two of the three wings, Bembridge, O. x 2. 4. *Clematis vectensis*, awned fruits, Bembridge, O. x 3. 5. *Radermachera pulchra*, winged seed, Bembridge, O. x 3. 6. *Apocynospermum dubium*, seed with pappus, Bembridge, O. x 12. 7. *Betula nana* (Arctic birch), leaf, Cambridge (Arctic-bed) x 6.8. 8. *Araucarites gurnardi*, leaf-cuticle, Bembridge, O. x 120. 9. *Azolla prisca*, male spore-mass, Bembridge, O. x 125. 10. *Azolla prisca*, male-spore, Bembridge, O. x 125. 11. *Diospyros antiqua*, calyx, Hordle, E. x 4. 12. *Ranunculus nemorosus* (buttercup), fruit, Swalmen, P. x 12.

13. *Trapa natans* (water-chestnut), nut, Brunssum, P. x 2. 14. *Fagus decurrens*, beech-mast, Reuver, P. x 2. 15. *Proserpinaca reticulata*, fruit, Reuver, P. x 2. 16. *Proserpinaca reticulata*, transverse section of fruit showing 3 locules, Brunssum, P. x 12. 17. *Nyssa silvatica* (American black gum-tree), nut, Swalmen, P. x 4. 18. *Corydalis pulchrum*, seed, Hordle, E. x 15. 19. *Atropa Belladonna* (deadly-nightshade), seed, Silchester, Roman x. 20. *Actinidia faveolata*, seed (outside) Brunssum, P. x 12. 21. *Actinidia faveolata*, seed (inside) Swalmen, P. x 12. 22. *Vitis vinifera* (grape), seed (ventral side), Tegelen, P. x 3. 23. *Vitis vinifera* (grape), seed (dorsal side), Tegelen, P. x 3.



Pteridosperms form a large and varied group but agree in having fern-like fronds and secondary woody thickening as a normal feature in their vascular construction. *Lyginopteris Oldhamia* the most completely known Pteridosperm is of Upper Carboniferous age and is of common occurrence in the coal-measures round Oldham and other parts of Lancashire. It is found petrified in the coal-balls and also as impressions in the shales forming the



BY COURTESY OF THE COUNCIL OF THE ROYAL SOCIETY AND OF PROF. OLIVER

FIG. 16.—SEED AND HUSK OF LYGINOPTERIS

A. Reconstruction of the seed in its husk. B. Seed and husk cut longitudinally

roofs of the seams. The frond (Plate I., fig. 3) by an equal forking of the leaf-stalk is divided into two equal divisions. The stem (fig. 15) varies from 2 mm. to 4 cm. in diameter. There is a pith forming the core of the stem surrounded by a ring of scattered vascular strands which are connected with the leaf supply system. In older stems the ring of strands is surrounded by a considerable quantity of secondary wood and bast. The outer cortex contained long anastomosing bands of fibres which formed a reticulum just below the epidermis. In *Heterangium*, a closely allied genus the centre of the stem is occupied by a solid core of primary xylem and the strands of the leaf-trace system were incorporated in the outer part of the primary xylem. Oliver and Scott in 1903 were able to identify a petrified seed found in a coal-ball, as the seed of *Lyginopteris* by the presence on its husk of glandular spines exactly like those on the frond and stems of *Lyginopteris*. The seed, *Lagenostoma Lomaxi* (fig. 16 A and B), is enclosed in a lobed husk or cupule; it is barrel-shaped and its integument is furnished with a vascular system. One part of the nucellus (sporangium wall) is modified to form a complicated pollen chamber or cavity in which the pollen became lodged. In structure the seed is very similar to those of the living Cycads or Ginkgo but the pollen-chamber is rather more complicated than any of these living plants. Kidston described some tassels of microsporangia (fig. 17) attached to small pieces of fronds which bore leaflets of the same shape as those of *Lyginopteris* and there is no doubt that they represent the pollen producing organs of this plant. In most seed-bearing plants the microsporangia are borne on highly modified structures, stamens, which are quite unlike leaves in appearance; but in many Pteridosperms the fronds which bear the microsporangia are very like the sterile foliage fronds and in this respect the Pteridosperms are primitive.

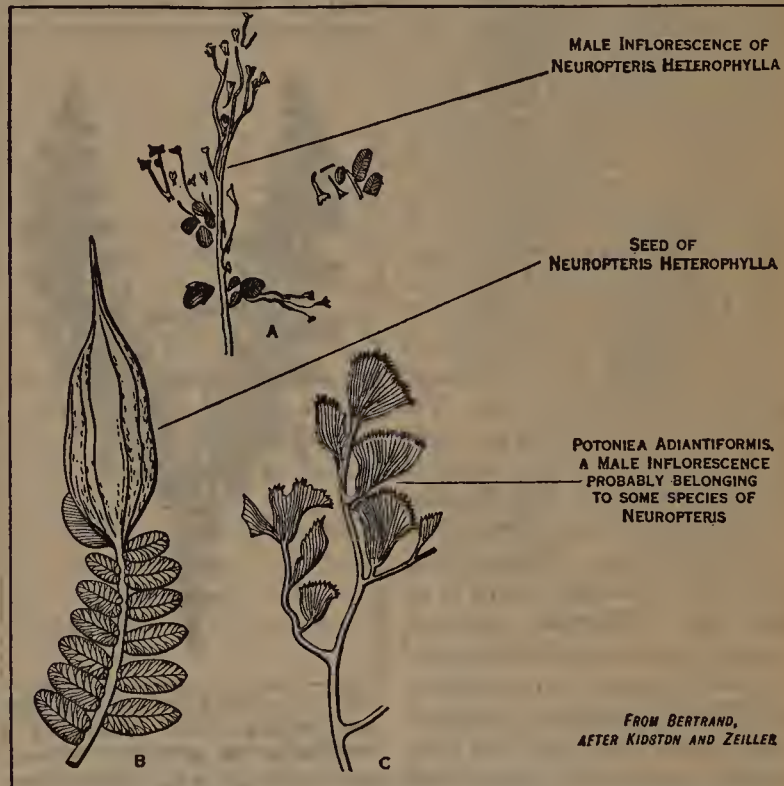
The *Medulloseae*, another important group of Pteridosperms, of Carboniferous and Permian age had fern-like foliage belonging to the form-genera *Neuropteris* and *Alethopteris*. The stems, *Medullosa*, which are known to belong to the group are peculiarly complicated in structure; in place of the usual single vascular column they had several. Each vascular column was in structure

like that of *Heterangium* and the stem could be briefly described as a polystelic *Heterangium*. The spirally arranged leaf stalks are of large size and contain a large number of small collateral vascular strands. The appearance of these petioles in section has given rise to the erroneous report that Monocotyledonous Angiosperms were present in the Carboniferous; they are however very like the petioles of *Stangeria*, one of the living Cycads. Another genus *Sutcliffia* had a large central stele with other smaller ones forming a system of meshes round it. Seeds have been found attached to fronds of *Neuropteris* (fig. 18, B) and *Alethopteris*. *Trigonocarpon* is a genus of seeds which were borne on some species of *Alethopteris*; it resembles the seeds of living Cycads in having a testa consisting of both soft and stony layers. The micropyle was of very considerable length. The pollen-producing organs of these plants (fig. 18, A and C) are still imperfectly known. *Pottonia* (fig. 18, C) very probably represents the pollen-bearing flower of a *Neuropteris*. The structures with toothed margins were originally cup-shaped with microsporangia placed on the inner surface of the cup. *Linopteris* an allied frond-genus had similar microsporangiate fructifications. Another fructification *Whittleseyia* had large cups more than an inch deep and large pollen grains have been isolated from them. In *Telangium* the microsporangiate fructification consists of synangia of from 6 to 25 fusiform sporangia attached to small terminal expansion of the divisions of the fertile frond. In *Telangium bifidum* and *Telangium teilianum*, both from the Lower Carboniferous, the fertile part of the frond branched repeatedly at wide angles. In *T. teilianum* the fertile part was at the extremity of the frond (fig. 19) and two large pinnae branching off from the rachis on either side acted as the foliage part of the frond. Several specimens have been found in which there is a small abortive branch in place of the fructification and the frond was entirely vegetative in function. In *T. teilianum* the pollen producing synangia are known to have been carried on the frond in this manner while in *T. bifidum*, a closely related species small seed-husks have been found similarly



FROM SCOTT, "STUDIES IN FOSSIL BOTANY" (A & C BLACK)

FIG. 17.—CROSSOTROCHA HOENINGHAUSI  
Male fructification of *Lyginopteris*



BY COURTESY OF (A) THE ROYAL SOCIETY AND PROF. OLIVER, (B) THE DIRECTOR OF THE SOCIÉTÉ GÉOLOGIQUE DU NORD, (C) THE SOCIÉTÉ GÉOLOGIQUE DE FRANCE: COPYRIGHT H. BONNAIRE

FIG. 18.—PTERIDOSPERM FRUCTIFICATIONS

placed. The nature of the stems of *Telangium* is unknown.

A large number of fossil-stems are known which, judging from their general structure, in all probability belong to the Pteridosperms. Nothing is known about their reproduction. In *Megaloxylon*, an Upper Carboniferous genus, the vascular cylinder consisted of a solid core of primary wood. The protoxylem elements are found in groups at the periphery and when followed upwards each group passes out to a leaf. On tracing them down-



wards each group spreads laterally round the stele in a tangential direction and finally becomes indistinguishable from the rest of the primary wood and so disappears. There was a considerable development of secondary wood round the primary cylinder.

The *Calamopityeae*, from the Lower Carboniferous though possibly also represented in the Upper Devonian, have in the centre of the stem a mixture of tracheids and parenchyma surrounded by a ring of xylem strands in each of which the first differentiated tracheids are in the centre. Surrounding the ring of strands is a sheath of secondary wood. The vascular supply to the leaf separates from one of the large xylem strands as in *Lyginopteris* and then divides further out into two strands each of which is surrounded by its own zone of secondary wood. This massive type of leaf supply is particularly characteristic of the Pteridosperms and is unlike the comparatively slender leaf-supply in the Gymnosperms. In the *Protopityeae*, unlike all plants known to be Pteridosperms, the leaves were arranged in two opposite series as in some species of *Psaronius*. The pith is elliptical with a sheath of primary xylem surrounding it. The leaf vascular supply is given off from the ends of the ellipse. Secondary xylem was present. Of more particular interest are the stems included in the *Cladoxyleae*. *Cladoxylon scoparium* (fig. 20) from the Middle Devonian of Germany is polystelic like *Medullosa* and the leaves which have been found in this species are deeply cleft and twig-like and are only  $\frac{3}{4}$  inch in length. The fertile leaves are not so deeply cleft and each division has a small terminal sporangium. Other *Cladoxyla* are known from the Lower Carboniferous; several have secondary thickening. There still remains some doubt about the systematic position of *Cladoxylon* which may be either a Fern or a Pteridosperm.

**Gymnosperms.** (Cordaiales, Coniferales, etc.)—*Cordaiales*. The Pteridosperms although they produced seeds had some very obvious features of agreement with the ferns: in the Cordaiales on the other hand there is little in common with the ferns and they may be regarded as fairly typical gymnosperms. There are three families provisionally grouped in the Cordaiales, the Poroxyleae, Pityeae and the Cordaiteae. *Cordaiteae*, the type genus of the Cordaiteae, of Carboniferous and Permian age, was a lofty tree (fig. 21), unbranched except near the summit and bearing large leaves, linear or spatulate in shape. The leaves are traversed with numerous parallel veins and must have looked somewhat like the leaves of the *Aspidistra*; they are inserted in spiral sequence on the stem and branches. The name *Noeggerathiopsis* has been given to similar leaves found in the Carboniferous and Permian of the Southern Hemisphere where the Southern type of Palaeozoic flora is found: there is no important difference between them and leaves of *Cordaiteae* and a separate name seems unnecessary. The inflorescences consist of small lateral branches each bearing numerous small catkins. Each catkin is about a centimetre long and has a short stout axis. In the staminate catkins the microsporangia are borne in bunches of from two to five at the ends of slender filaments which contained vascular tissue. These filaments bearing the sporangia arise from between the small, crowded scale leaves which formed the bulk of the catkin or were grouped together near the top. The pollen grains found in the sporangia are of large size. The ovulate or seed producing catkins like the staminate were formed of closely imbricating scales. Short stalks bearing ovules arose at intervals between the scales and according to one investigator corresponded in position

to scales. In some specimens these stalks were very short but in others the seeds are found hanging out of the catkins on elongated stalks. It is possible that the stalk of the ovule lengthened as the ovule developed into a seed. The ovules and seeds are flattened in a plane tangential to the catkin. The integument of the ovule consisted of a hard inner layer and a fleshy outer layer while the

nucellus had a well developed pollen chamber with a canal leading to it and was much like the nucellus of the living *Cycas*. In the pollen-chamber large pollen grains have been found similar to those found in the microsporangia. The stem is constructed like that of a conifer except that the pith is much larger and consisted of soft tissue which split transversely into a series of diaphragms in the older condition of the stem. When the stems started to decay these diaphragms broke down and internal casts in sandstone of these pith cavities exhibit transverse grooves which correspond to the remains of the diaphragms at the edge of the pith. These casts receive the distinguishing name *Artisia* and it is not always possible to say whether they belong to *Cordaiteae* itself or to some nearly allied genus. The wood is entirely

trifugal in *Cordaiteae* but in the closely allied genus *Mesoxylon* there was a small amount of centripetal primary wood. The primary strands project into the pith. In cellular organisation the wood is very like that of the living *Araucaria* but like most other Palaeozoic woods from the Northern area there is no evidence of seasonal periodicity in the growth as indicated by the presence of "annual rings." The vascular supply to the leaf is represented by two of the primary strands surrounding the pith, which at higher level pass outwards and on reaching the base of the leaf fork repeatedly and link up with the numerous veins of the leaf lamina. This double vascular connection with the axis is also found in *Ginkgo* (maiden hair tree) and is also found in the Pteridosperms. [In the structure of the leaf some species of *Cordaiteae* show close resemblance to the cycads, for in each vein the xylem is in two parts; the larger strand lying next the upper surface of the leaf consisting of centripetally developed secondary wood while the underlying strand is centrifugal with the bast lying immediately below it. In other species there is no strand of centrifugal wood. [Both these types of vein are found in the living cycads sometimes in the same leaf for the base of a cycad leaf centrifugal xylem may be present while higher up it may completely disappear.] The veins in some species are surrounded with a sheath of cells with bordered pits just like the corresponding tissue in the leaf of the cycads. Thus in *Cordaiteae* we find a remarkable combination of pteridosperm, cycad and conifer characters. The fossil roots called *Amyelon radicans* though as yet they have not been found actually attached to the rest of the plant from their almost constant association and agreement in certain microscopical characters are almost certainly parts of cordaitean plants. They are typical gymnosperm roots and some of the smaller ones have been found to be infested with fungal mycelium. From the position of the fungus in the roots it is almost certain that they afford an example of the association of a fungus with the higher plant which is common in living gymnosperms as well as in some of the angiosperms and is called Mycorrhiza (*q.v.*). The leaves of the Poroxyleae, a Permian family, attained the length of a metre and a fifth of a metre in width and show resemblance in structure to leaves of the cycads. The branches arise in the axils of the leaf as in some species of *Lyginopteris* while the vascular tissue of the branch



FROM KRAUSEL UND WEYLAND, "DEVONFLORA" (SENCKENBERGISCHE NATURFORSCHENDE GESELLSCHAFT)

FIG. 20.—CLADOXYLON SCOPARIUM This is a Middle Devonian plant from Germany, with a very complex type of vascular organisation



FIG. 19.—FROND OF A LOWER CARBONIFEROUS PLANT, PROBABLY A PTERIDOSPERM, WITH THE TELANGIUM TYPE OF MALE FRUCTIFICATION (1/3 NATURAL SIZE)



connects up with that of the stem as in the pine. Structurally the stem is more like *Lyginopteris* than *Cordaites*. The xylem of the primary bundles surrounding the pith is entirely centripetal. Where the vascular tissue to the leaf connects with the vascular tissue of the axis it consists of two bundles similar in construction to those of cycad leaves. When traced further down the stem these two bundles appear to fuse and still lower they are only rep-



AFTER GRAND EURY IN SCOTT, "STUDIES OF FOSSIL BOTANY" (A & C BLACK)

FIG. 21.—RESTORATION OF A CORDAITES TREE, SHOWING ROOTS, TRUNK, AND BRANCHES BEARING LONG LANCEOLATE LEAVES AND FRUCTIFICATIONS

resented by a strand of secondary xylem. In the Pityeae, a Lower Carboniferous and Upper Devonian group, while there are characters indicating a relationship to the rest of the Cordaitales there are also features in their construction which mark them out as a rather distinct group. *Pitys Dayi*, a plant of arborescent habit from Lower Carboniferous rocks on the shore of the Firth of Forth, had short conical projections on its branches representing the leaves which had no flat, expanded surface. These short squat leaves must have made the tree appear like a coarse *Araucaria excelsa*. The stem had a wide pith with a ring of vascular bundles near the periphery with other smaller bundles scattered through it. The first differentiated elements are in the centre of these bundles. The relation between these strands and the rest of the vascular system is unknown. The lower part of the bundle supplying the leaf was situated in the peripheral ring and the upper part forked into three strands in the base of the leaf. A zone of secondary wood surrounded the ring of primary strands but was separated from them by a narrow zone of parenchymatous tissue. Nothing is known about the fructifications of these plants. In *Callixylon* an Upper Devonian genus there are no scattered bundles in the pith but otherwise the structure is not unlike that of *Pitys*. There is little doubt that *Callixylon* and *Pitys* are closely allied. Although an older group than the Cordaitae and Poroxyleae the Pityeae show closer resemblance to the Araucarian conifers and less evidence of affinity to the Pteridosperms and cycads. A con-

sideration of the comparisons that have been made between these groups leads to the belief in a common ancestral group from which they have all descended.

**Coniferales.**—The conifers are the most important group of living gymnosperms and there is evidence of their existence as early as the Palaeozoic. *Walchia* which appears in the Upper Carboniferous, though typically a Permian genus, had leaves and branches very like those of *Araucaria excelsa*. Casts of the pith cavity which show the course of the primary bundles show that in organisation the stem was also in substantial agreement with *Araucaria*. Cones have been found on the ends of the twigs of some species and R. Zeiller has shown that the seeds were in one species borne singly on the cone-scales, a distinctly Araucarian character. More is known about *Voltzia* a characteristic Permian and Triassic genus. The foliage shoots (fig. 22 A) of some species are much like those of *Walchia* and *Araucaria excelsa* and show the same variability in size of leaf even on closely adjoining portions of the same twig. The ovulate or seed-bearing cones (fig. 22, B) are built up of spirally arranged loosely packed scales. Each seed-bearing scale in the Permian species *V. Liebeana* (fig. 22, C, D) had three main lobes, each with a seed attached to its upper surface near its base, and two smaller lobes alternating with the three main lobes but set slightly behind them. In one specimen of a scale which has been investigated a thin pointed scale is present attached to the back of the lobed scale (fig. 22, D). The presence of this scale is of interest in considering the interrelationship of the different groups into which the living conifers are classified and in estimating their relative antiquity. In the Abietineae, the group of conifers to which the pine, cedar, larch, etc., belong, the cone is built up of two kinds of scales each with a vascular system of its own, sterile bract-scales and seed-scales which are situated in the upper angle between the bract scale and the axis of the cone and are partly coherent with the former. In the Japanese cedar (*Cryptomeria*) the two scales are coherent for a greater part of their length and only the tips are free. In others again e.g., *Sequoia* (giant tree of California) there is no outward evidence that two scales are present but the apparently single scale has a double set of vascular bundles which reveal its fundamentally double nature. In the Araucarineae the scale shows practically no indication of being double. For this reason and because the Araucarineae differ in many other ways from the rest of the Coniferae it has been suggested that they have had a separate ancestry from the others. It would appear however from a consideration of the type of double scale found in *Voltzia* which is otherwise very like an *Araucaria* that these two divisions of the Coniferae may have diverged from a common ancestral group which was represented in Permian and Triassic times by plants of the *Walchia* and *Voltzia* type.

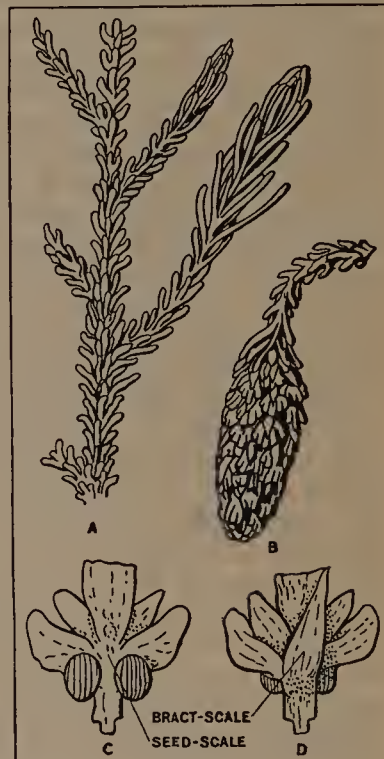


FIG. 22.—VOLTZIA; A PALAEOZOIC CONIFER

A. Leafy twig. B. Seed-cone. C. Ventral face of seed-scale with two seeds. D. Dorsal face of seed-scale, with adherent bract-scale

**The Distribution of Palaeozoic Floras.**—We have seen that the Predevonian Floras consist of Thallophytes, either marine or fresh-water, and we have no evidence of a land vegetation until after the close of the Silurian Period. In the Devonian there is evidence of a rich vegetation from as far north as Ellesmere land and Spitsbergen and as far south as the Falkland islands; so that either the distribution of climatic zones fluctuated considerably or else the climate of the earth was more uniform. The former seems to be the more likely hypothesis. In the Lower



Devonian some large Thallophytes are still found, e.g., *Nematophyton*, while *Zosterophyllum*, *Psilophyton* and *Arthrostroma*, also characteristic of the period, may represent transition types between Thallophytes and Pteridophytes, but are distinctly nearer in their affinities to the latter. In the Middle Devonian more complicated types appear and in the Upper Devonian several groups of a more modern aspect such as the Lycopods and Ferns become distinct. In the Lower Carboniferous the important groups are the Pteridosperms, Lycopods, Equisetales and ferns and with this constitution the flora persists right through the rest of the Carboniferous and Permian. In the Upper Carboniferous there is evidence of a change of a far reaching nature in the southern hemisphere for a different flora is found there from that in the north. This difference was probably connected with the glacial period which prevailed in the south in Carboniferous times and which left unmistakable traces in contemporary rocks in South Africa and Australia. This southern flora, characterized by the fern-like plant *Glossopteris*, extended into parts of Russia and India but the greater part of the northern hemisphere had an Upper Carboniferous flora of the west European type. An outlier of the northern type of flora has been found in Carboniferous rocks in Sumatra, while in northern South America and in South Africa there is evidence in rocks of the same age of a flora of an intermediate type.

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### MESOZOIC

**Introductory.**—The middle period of geological history, which embraces a succession of ages extending over a few hundred million years, is known as the Mesozoic era; it is divided into three periods, the oldest or TRIASSIC period, followed by the JURASSIC and CRETACEOUS periods. The term RHAETIC (from the Rhaetian Alps) is used for the stage of earth-history between the Triassic and Jurassic periods. Before considering the march of plant-life through the Mesozoic era, it is desirable to obtain a general idea of the relation of the world's vegetation as it was at the beginning of the middle period and of the broad features of the vegetation which has been reconstructed from the remains preserved in the rocks of the post-Mesozoic or Cainozoic era. We shall then be in a better position to appreciate the relation of the floras with which we are now concerned to those which preceded and followed them. In the course of the Palaeozoic era a large portion of the earth's surface had become colonized by many different kinds of plants; some of them comparatively simple, others rivalling in the complexity of form and structure forest trees of the present day. These ancient land-plants were in all probability the modified descendants of inconceivably remote ancestors which lived in the primeval seas. A botanist familiar with the vegetation of to-day, if he could wander through the forest-covered swamps of the latter part of the Carboniferous period (the Coal age), when the Palaeozoic floras reached the zenith of their luxuriance, might at the first glance think himself in a world where tree ferns, giant horsetails (*Equisetum*) and club mosses (*Lycopodium*, etc.) played a dominant part, but on closer inspection he would find that the great majority of the plants were in many respects far removed from all modern types. If he travelled across what are now Europe and North America and extended his journey into the Arctic regions, he would discover comparatively few well marked differences between the western and eastern floras in this area. He would see certain plant-associations on the drier ground and others occupying the low-lying swamps, but the vegetation as a whole would not show any well defined contrasts. Were he to travel into central China and to the Malay region he would be struck by the general resemblance of the dominant plants to those in the northern hemisphere. We know that the forests of the Coal age included many extinct members of the class Pteridophyta (ferns, horsetails, club mosses, etc.) which in their tree-like dimensions and in other characters differed widely from the corresponding diminutive plants of our own time. We know also that

nearly all the fern-like shrubs and trees were not true ferns but plants for which it has been necessary to institute a new group-name, the Pteridosperma (see Palaeozoic section, above), because they produced seeds in place of the spore-cases (sporangia) which are characteristic of modern ferns. Some of the trees were similar in habit and in the structure of the wood to existing members of the *Araucaria* family, but they differed from all living gymnosperms in the nature of the reproductive organs. There were a few plants with leaves agreeing in form with the fronds of cycads, the surviving representatives in the vegetation of the present day of the Cycadophyta, a class which played an increasingly important rôle as the Mesozoic floras succeeded one another. Similarly a wanderer in the Palaeozoic forests would note here and there trees with relatively broad, wedge-shaped leaves resembling in form and in venation those of the maidenhair tree (*Ginkgo*). In the absence of flowering plants (Angiosperms) and in the unfamiliar features of most of the commoner trees, the forests of the Coal age formed a striking contrast to the woodlands of the modern world. The vegetation of the latter part of the Carboniferous period persisted in diminished numbers into the Permian period which is the last chapter of Palaeozoic history. At the close of the Carboniferous period changes in the earth's crust, which were sufficiently widespread and disturbing to be described as a geological revolution, created a new environment; humid swamps were transformed into relatively dry and hilly regions or into arid wastes in which inland seas like the Caspian replaced estuaries and fresh-water lakes. This shifting of the geological background is reflected in the clearly marked change in the character of the vegetation. The plants from Permian rocks are less numerous and less varied than those preserved in the coal seams and associated sediments of the latter part of the Carboniferous period. At the end of the Palaeozoic era the development of the plant world suffered a severe check; many of the Carboniferous trees failed to survive; a few new forms were evolved, but on the whole there was no marked alteration in the main botanical features of the depauperated floras.

Leaving the threshold of the Mesozoic age we may glance for a moment at the records of plant-life preserved in the rocks classed by geologists as Cainozoic or Tertiary, the rocks which chronicle the events between the Mesozoic era and the relatively short period which began with the great Ice age and shades imperceptibly into the historical age. The vegetation of the Cainozoic era was practically identical in its general composition with that of tropical and sub-tropical lands at the present day. Then as now flowering plants (Angiosperms) were the ruling dynasty and the majority of gymnosperms, ferns and other groups were essentially similar to their descendants which flourish at the present day.

The Palaeozoic forests were archaic and unfamiliar; those of the Cainozoic periods were definitely modern. This transformation was effected during the Mesozoic era; it is therefore in hopeful expectation that the student of ancient floras turns to the fragmentary samples of the vegetable world preserved in the rocks of the intervening epoch of geological history. From a study of Mesozoic floras we might expect to be able to connect the portions of the chain of life reconstructed from Cainozoic fossils with the much more ancient pieces disinterred from Palaeozoic strata. While it is true to say that palaeobotanical research has contributed much towards a knowledge of the successive floras of the Mesozoic era, it is equally true to say that we are still groping after clues which may eventually enable us to visualize the sequence of events in the course of the middle or critical stage in the history of the plant-world. The chief purpose of this article is to present in as concise a form as possible the evolutionary tendencies in the course of the long ages separating the Palaeozoic from the Cainozoic era, so far at least as they can be discovered from the meagre documents at our disposal. The imperfection of the geological record is well put by Sir Joseph Hooker: "We have not in a fossilized condition a fraction of the plants that have existed, and not a fraction of those we have are recognizable specifically."

So far no reference has been made to the Palaeozoic vegetation in the southern hemisphere. In order to obtain as complete a picture as possible of the immediate antecedents of the earliest Meso-



zoic floras it is necessary to include in our summary the greater part of the earth's surface on which we have any information. Owing to the difficulty of defining the boundary in some regions between the Carboniferous and Permian plant-beds it has been a common practice to employ the term Permo-Carboniferous as an admission of incomplete knowledge. We have already given a brief account of some of the salient features of the Permo-Carboniferous vegetation in the northern hemisphere. It is generally agreed that on the northern continents at the close of the Carboniferous period the climatic conditions were genial and favourable to the development of a luxuriant vegetation, and that in the course of the Permian period folding of the earth's crust produced changes in the physical setting which reacted disastrously on the plant-world. We cannot separate the organic from the inorganic world; evolution must be considered from a double aspect, the evolution of the plants in relation to a changing environment.

**The *Glossopteris* Flora.**—A precise correlation of beds in widely separated parts of the world is by no means easy; we cannot, for example, assert with confidence whether or not a flora revealed by a study of late Palaeozoic rocks in India and the southern hemisphere was actually contemporaneous with the forests of the northern hemisphere Coal age, or whether certain climatic conditions demonstrated by geologists in the lands south of the Equator synchronized with a strongly contrasted climate in the North. There is, however, a strong body of evidence in support of the view that before the close of the Carboniferous period, when large areas on the northern continents were covered with forests, the southern lands were in the grip of an Ice age and supported a sparse vegetation markedly different from that found on the northern swamps. In the early days of the Carboniferous period closely allied or even specifically identical plants grew in the Arctic regions, in Australia and in many other widely separated regions; the vegetation seems to have been remarkably uniform. In the later stages of the period, on the other hand, there was a well marked differentiation into two or more botanical provinces occupied by more or less sharply contrasted floras. In the latter part of the Palaeozoic era there were two large continents in the northern hemisphere, one including North America, Greenland and Europe which is sometimes spoken of as *Eria*; and another embracing a large part of Siberia known as *Angara Land*. Beyond the world-encircling *Tethys* sea, which washed the southern shores of these great continents, was the vast continent of *Gondwanaland*, formed of what are now India, Australia, Africa and South America. In geological maps *Gondwanaland* is usually shown as a continuous land mass parts of which are assumed to have foundered. If we adopted the hypothesis of Wegener, *Gondwanaland* would have to be represented as a portion of the crust formed of the present southern continents and India fitted into one another like pieces of a jig-saw puzzle. From this compact mass, disrupted in the Mesozoic era by deep fissures, huge blocks slowly drifted away, like icebergs from a glacier, until they reached their present positions. The Permo-Carboniferous plants and sedimentary rocks of *Gondwanaland* indicate a state of affairs in the organic and inorganic worlds very different from that revealed by the records in the northern hemisphere. In New South Wales, for example, rocks containing remains of Lower Carboniferous plants agreeing closely with northern species are succeeded by thick masses of old boulder clays (*tillites*) which afford convincing evidence of a glacial period at the close of the Palaeozoic era, a reign of ice probably longer and more widespread than that which in comparatively recent times held sway over North America and Europe. Geological investigations in Australia have established the fact that before the end of the Carboniferous period the earth's crust was uplifted into mountain-ranges and conditions were produced favourable to the accumulation of ice and snow. Throughout geological history there were recurrent cycles of mountain-building and shifting of the scenes which produced new sets of factors conditioning plant-life; revolutions in the inorganic world caused transformations in the organic world. The story told by the series of plant-beds and glacial deposits in Australia, though differing in detail from that derived from a study of the corresponding strata in India, South America and Africa is broadly

speaking the same for *Gondwanaland* as a whole. Beds of boulder clay containing innumerable erratic blocks, often many tons in weight and resting on platforms grooved and striated by slowly moving rock-studded masses of ice, occur over thousands of square miles from one end of *Gondwanaland* to the other, from the Falkland Islands to Tasmania, from northern Australia to Afghanistan. The approximate areas which are occupied by glacial beds are indicated in the map. The discovery of plant remains in the Argentine and in South Africa at the base of the glacial beds shows that in these regions, as probably elsewhere, the climatic conditions were not fatal to the existence of vegetation.

*Gondwanaland* towards the close of the Palaeozoic era may be compared with Alaska and Greenland at the present day, where glaciers and ice-sheets are bordered by an Arctic vegetation. One of the commonest Permo-Carboniferous plants on the southern continent was the genus *Glossopteris* (fig. 1), so named from the tongue-like form of the leaves, the larger of which reached a length of more than a foot. From a well-defined mid-rib are given off arching veins which by repeated unions form a fairly regular network. *Glossopteris* was formerly regarded as a fern similar in its fronds to the existing hart's tongue (*Scolopendrium*) but differing from it in the architecture of the venation; it is now believed to be a member of the Pteridosperms (*see above*.) Seeds and leaves have not been found in organic union, but their frequent association in the rocks and the discovery of certain other pieces of evidence favour the conclusion that the stems which bore *Glossopteris* leaves bore also seeds. Because of the abundance of *Glossopteris* fronds and pieces of the stems (*Vertebraria*) the flora of *Gondwanaland* is usually spoken of as the *Glossopteris* flora. Another common genus is *Gangamopteris* with leaves on the whole larger than those of *Glossopteris* and distinguished by the feeble development or absence of a mid-rib: the two forms of leaf are not always easy to separate. Both genera are almost certainly Pteridosperms. *Schizoneura* is also a characteristic southern genus: more robust than *Equisetum* but similar to the horsetail in its jointed stems, it is distinguished from the northern hemisphere *Calamites* by its longer and broader leaves coalescent in varying degrees into a sheath which enveloped the foliage-shoots at each node. The genus *Neuropteridium* (*Gondwanidium*) (fig. 2) is represented by simple pinnate fronds superficially resembling those of some modern ferns and characterized by the large lobed leaflets; from the lack of fertile leaves one suspects that it may be a Pteridosperm. Two sets of fronds have been called *Neuropteridium*, Permo-Carboniferous and Triassic fronds. It has recently been suggested that, as there is no satisfactory evidence of generic identity, the older forms should be renamed *Gondwanidium*, *Neuropteridium* being reserved for Triassic fronds (fig. 11), which were probably borne on ferns and not on Pteridosperms. These four genera do not occur in the later Carboniferous or in the Lower Permian floras on the continents north of the *Tethys* sea. The *Tethys* was a broad sea, stretching across the world. The Mediterranean is its diminutive modern representative. The discovery in 1912 of *Glossopteris* and thin beds of coal by the heroic members of the second Scott expedition on the Beardmore glacier, 3000 m. from the South Pole, points to the existence of this plant far within the Antarctic circle. It also suggests the possibility that *Glossopteris* and perhaps some of its associates had their origin in the far South.

With the more typical and more abundant members of the *Glossopteris* flora are associated in some regions, plants generically indistinguishable from northern forms. The long strap-like leaves originally described as *Noeggerathiopsis*, similar in size and shape to the foliage of *Yucca*, appear to be the foliage of trees closely allied to the common northern genus *Cordaites*. Similarly a few species of *Sigillaria* and *Lepidodendron* are recorded from South Africa and South America in company with *Glossopteris*. Other genera which afford points of contact between the two great botanical provinces are *Psaronius*, recorded from Brazil, a tree-fern allied to the tropical Marattiaceae in modern floras; the genus *Sphenophyllum* discovered in India, South Africa and Australia, *Psymphyllum* with wedge-shaped, lobed leaves similar in form to those of *Ginkgo biloba* (the maidenhair tree) but not neces-





FROM (1) "CATALOGUE OF FOSSIL PLANTS OF THE GLOSSOPTERIS FLORA," (2, 4) DU TOIT, "UPPER KARROO FLORA," (3, 7) "CATALOGUE OF THE WEALDEN FLORA," (5) WALLACE, "MALAY ARCHIPELAGO" (MACMILLAN), (11) ZITTEL, "SEPARAT-ABDRUCK AUS PALAEOGEOGRAPHICA," IN "DIE FOSSILE FLORA DES BUNTSANDSTEINS" (SCHWEIZERBART)

FIGS. 1-11.—EXAMPLES OF MESOZOIC PLANTS AND TWO LIVING FERNS CLOSELY RELATED TO CERTAIN MESOZOIC FERNS

1. Two forms of *Glossopteris* (A  $\frac{1}{2}$  nat. size, B nat. size). 2. *Neuropteridium*, probably a Pteridosperm, slightly less than nat. size. 3. Branch of *Podozamites*,  $\frac{2}{3}$  nat. size. 4. Fronds of *Thinnfeldia* (A slightly reduced, B slightly enlarged). 5. *Matonia* (taller) and *Dipteris*, ferns, much reduced. 6. Cycadean frond,  $\frac{1}{2}$  nat. size. 7. Two leaves of *Sagenopteris* (A nat. size, B slightly enlarged). 8. Fruits believed to belong to *Sagenopteris*. 8a. Restoration of *Griethoropia Nathorati*, nearly twice nat. size. 8b. *Caytonia Sewardi*, fruct. 8c. *Caytonia Sewardi*, longitudinal section. 9. Stem of *Cycadeoidea gigantea*,  $\frac{1}{3}$  nat. size. 10a. Restoration of an unexpanded inflorescence, nat. size. 10b. Surface-view of seed-bearing centre (conical apex in 10a). 11. Fronds of *Neuropteridium*, attached to stem.  $\frac{1}{4}$  nat. size

sarily a member of the same class; also a few fern-like fronds which are probably Pteridosperms.

Apart from the abundance of *Glossopteris*, *Gangamopteris* and some other genera peculiar to the Gondwanaland flora, the most striking distinctive feature of the southern vegetation is the absence of the great majority of species and of many genera which played a prominent part in the northern forests. The important point is that the flora of Gondwanaland was relatively meagre and the commonest plants were peculiar to the southern province at least up to the time of the middle of the Permian period. Several years ago some leaves of *Glossopteris* were found in beds of Upper Permian age in northern Russia; more recently this and other

members of southern flora have been recorded from several localities in Siberia, also remains of an Upper Permian flora which differed from contemporary floras in the northern hemisphere in the admixture of Gondwanaland species with plants characteristic of the northern province. This Kusnezsk flora, so called from the locality in Siberia, has been traced from northern Russia through Siberia and north-west Mongolia to the coast at Vladivostok: it includes with *Glossopteris* such genera as *Neuropteris*, *Callipteridium*, and *Lepidodendron* represented by species characteristic of the northern province. With the Palaeozoic species agreeing with northern or southern forms it is of special interest to find some genera which are characteristic of Mesozoic



floras: examples of these are species of *Baiera*, *Phoenicopsis*, *Czekanowskia*, all members of the Ginkgoales, characteristic of pre-Cretaceous Mesozoic floras and more or less closely allied to the maidenhair tree; also *Podozamites* (fig. 3), a genus of uncertain affinity but a gymnosperm probably similar in habit to recent species of the conifer *Agathis* (the kauri pine, etc.) which was very widespread in the earlier Mesozoic floras; *Voltzia*, a conifer, simulating in its leaves some living *Araucarias*, characteristic of Permian and early Triassic floras in the northern hemisphere and recorded from the *Glossopteris* flora of India, also *Dioonites*, a genus founded on cycad-like fronds similar to those of the existing Mexican genus *Dioon*. The discovery of beds containing Kusnezsk species on the coast of Ussuri Land overlain by strata containing the typical Lower Triassic genus *Pleuromeia* indicates a Permian age for this widespread flora despite the occurrence of several Mesozoic types. There must have been a northward migration of *Glossopteris* and some of its companions across the Tethys sea either by a chain of islands or by a land-bridge. The genus *Glossopteris* is one of several genera which probably originated in the southern hemisphere and gradually spread across the Equator; by the end of the Permian period it was firmly established in the province of the Kusnezsk flora and it has recently been recognized in the Rhaetic flora of Scoresby Sound, which is in east Greenland. Similarly the occurrence of *Schizoneura* in the early Triassic flora of western Europe illustrates the penetration of members of the *Glossopteris* flora into the northern hemisphere in the early part of the Mesozoic era.

It has recently been shown that the Permian or Permo-Carboniferous vegetation of some regions in China was of the typical northern type. Prof. Halle of Stockholm in an exceptionally important memoir (1927) has given an account of the late Palaeozoic floras of central Shansi which are preserved in two series of sediments; the older strata known as the Yuehmenkou series and above it the Shihhotse series. Both floras included species of *Calamites*, *Sphenophyllum*, *Pecopteris*, *Callipteridium*, *Cordaites*, *Stigmara* and other northern Permo-Carboniferous types. As in the Kusnezsk flora so also in the collections from the Shihhotse series there are species belonging to genera such as *Cladophlebis*, *Neuropteridium*, *Chiropteris* and *Dioonites* which bear a very close resemblance to members of Triassic floras in many parts of the world. *Chiropteris* is a genus represented by broad leaves with forking and anastomosing veins which in form remind one of the fronds of some species of the fern *Ophioglossum*; its systematic position is uncertain. Specimens are recorded from Triassic beds in Germany, South Africa and elsewhere. The name *Cladophlebis* is given to the branched fern fronds bearing comparatively short and often slightly curved leaflets, with a central rib and arching, forked lateral veins, attached by the whole of the base; species are characteristic of many Mesozoic floras but are seldom met with in Palaeozoic floras. The Shansi floras differ from the Kusnezsk flora in the absence of *Glossopteris* and other Gondwanaland plants. The Shihhotse series is overlain by barren sedimentary beds indicative of desert conditions; it is highly probable, as Halle suggests, that in these beds we have evidence of a change from a genial and humid to a dry climate, which coincided in date with a corresponding revolution chronicled in the Permian period over a wide area in the northern hemisphere. Floras similar to those of Shansi are recorded also from Korea.

This incomplete presentation of facts may serve to illustrate some of the broad features in the distribution and composition of floras at the stage of geological history immediately antecedent to the Mesozoic era. There were at least three botanical provinces characterized by floras that were distinguished by the abundance of certain genera: (1) A very widely distributed and fairly homogeneous northern flora which probably had its origin in the lands north of the Tethys sea and spread southward into China and members of it reached the Malayan region as invaders of the realm of Gondwanaland; (2) the *Glossopteris* flora from which in late Permian days some of the plants wandered far to the north, and *Glossopteris* penetrated to Greenland well within the Arctic circle; (3) the Kusnezsk flora of Upper Permian age, which was in part composed of plants which had found their way across the

Tethys sea from the south and in part of representatives of northern Permian floras.

At the beginning of the Mesozoic era the prevalence of desert conditions over a wide area in North America and in the Old World was highly unfavourable to the further development or the continued existence of many members of the rich Permo-Carboniferous flora. By far the greater number of the Palaeozoic species failed to survive; a few new forms were evolved, and some plants such as *Schizoneura* and *Voltzia* were immigrants from Gondwanaland. A comparison of late Palaeozoic and early Mesozoic floras reveals a sharp contrast which furnishes an interesting illustration of the interdependence of organic and inorganic evolution, of the effect of changing geographical conditions on the evolution of the plant world. One of the well established conclusions of geologists is that there have been recurrent cycles of mountain-building and, as a necessary consequence, recurrent interferences with the factors conditioning plant life. One of these geological revolutions occurred at the end of the Palaeozoic era not only in the northern hemisphere but also in China and in some other regions. One of the more important aims of the student of evolution is to discover connecting links in the plant world, particularly at epochs of widespread crustal disturbances. Attention has already been called to the presence in late Permian floras of genera that are characteristic of Mesozoic floras: types, which became prominent in the latter part of the Triassic period and persisted through the several stages of the Jurassic period, were already in existence, though in a subordinate position, before the close of the Permian period. The greatest contrast between the two eras is the marked difference in the general facies of the vegetation consequent on the disappearance of most of the commoner members of the older forests; but there is also a considerable difference which is due to the relative abundance in the Mesozoic floras of plants of more modern aspect, plants that are closely akin to living species as contrasted with the more archaic and much less familiar types in the Palaeozoic floras. A comparison of the rich fern vegetation of the Upper Triassic and Rhaetic floras with the comparatively small number of true ferns in the Permo-Carboniferous vegetation raises a question which has not been fully answered; whence came the more modern types of ferns which characterize the Mesozoic floras? The late Palaeozoic ferns, apart from the Marattiaceae, which can be linked with Triassic and Rhaetic forms are very few, and the evidence they afford of direct relationship to Mesozoic ferns is not convincing.

**Triassic Floras.**—In a general account of the Mesozoic floras it would be out of place to discuss the precise geological horizons within the Triassic period of the plant-bearing strata in different parts of the world, but it is important to consider the composition of the earlier Triassic floras in contrast to the richer plant communities which characterize the later stages of the period.

Remains of early Triassic floras have been found at a few localities in Europe, notably in the Vosges district, on the northern edge of the Eifel, and elsewhere. Characteristic genera are *Pleuromeia*, *Schizoneura*, *Voltzia*, *Albertia*, *Pelourdea*, *Neuropteridium*, *Equisetites* and a few examples of Cycadean plants. *Pleuromeia* is represented by stems, occasionally reaching a length of 2 metres or more, with spirally disposed leaf-scars similar to those on some species of the older genus *Sigillaria*. On the upper region of the stem were overlapping, short and broad scales bearing seed-like reproductive organs. The lobed and swollen base of the stem bearing numerous rootlets suggests comparison with the living quillworts (*Isoetes*). We may picture the plant as a comparatively low unbranched shrub bearing needle-like leaves and at a higher level shorter and broader fertile scales, growing probably among sand dunes in arid regions. It is one of the rare links discovered in Mesozoic floras with the tree-like lycopodiaceous plants of the Coal age. Along with species of *Schizoneura* occur large stems of *Equisetites* differing in their ampler proportions and possibly in structure from modern horsetails. *Voltzia* is a conifer resembling in its foliage-shoots and in the structure of the wood species of *Araucaria*, e.g., the Norfolk Island pine, *Araucaria excelsa*, but in some respects differing from all recent conifers notably in the structure of the female shoots. *Albertia* with its broader



leaves recalling those of *Agathis*—the genus which includes the kauri pine of New Zealand—may also be related to the Araucarias. In Arizona over many square miles of country petrified trunks of trees, some probably 200ft. in length, have been laid bare by the denudation of early Triassic rocks; many of the stems are Araucarian or have Araucarian characters. Specimens of ribbon-like leaves have been described from Triassic beds as species of *Yuccites*, *Bambusium*, etc., because of their similarity to the leaves of *Yucca* and bamboos. It has been proposed to refer them to the non-committal genus *Pelourdea*. The probability is that these leaves were borne by plants descended from *Cordaites* or other Palaeozoic gymnosperms.

Reference has already been made to the fern-like fronds of *Neuropteridium* (*Gondwanidium*) as fossils characteristic of the Glossopteris flora; the name *Neuropteridium* is applied also to some Triassic leaves (fig. 11) which are probably not directly related to the southern and older examples. The occurrence of a few fronds such as *Dioonites* and *Zamites* in earlier Triassic floras prepares us for the rapid development of the Cycadophyta in the Rhaetic and Jurassic floras. It is, however, important to note that these generic names, suggested by the resemblance of the fossil leaves to those of the living Mexican and American Cycads *Zamia* and *Dioon*, should not be regarded as evidence of close affinity of the extinct to the living forms.

The much greater abundance and variety of plants in later as compared with the earlier Triassic floras affords evidence of amelioration in the physical environment. Collections made from the Richmond coal field in Virginia and from Upper Triassic beds in Austria and Switzerland enable us to follow the main lines along which the plant world was developing. Among equisetaceous types attention may be called to the genus *Neocalamites* which is not always readily distinguishable from *Schizoneura*. It is characterized by long linear leaves springing in circles from the nodal joints and free to the base instead of being united into a sheath as in *Equisetum*. *Neocalamites* was a very widely distributed Triassic genus; it is recorded from Tongking, from South Africa and Australia, as well as from northern localities. A notable feature of the Keuper floras is the abundance of ferns; *Macrotaeniopteris*, characterized by simple banana-like fronds reaching a length of a metre and a breadth of 17cm., is probably a fern though no sporangia have been discovered. Fronds often described as species of *Acrostichites*, an unfortunate name because of its implication of relationship to the living genus *Acrostichum*, are in some instances at least members of the Osmundaceae, a family which has been traced as far back as the Permian period. *Clathropteris platyphylla*, with its large fronds divided into spreading lobes like the segments of a horse chestnut leaf and its approximately rectangular meshes of slender veins on either side of a central rib, is one of many ferns in Mesozoic floras agreeing closely with the Indian and Malayan species of the genus *Dipteris*. The family Marattiaceae, now characteristic of the Tropics, was also represented by *Pseudodanaeopsis*, *Marattiopsis* and other genera closely resembling recent tropical species. These and other ferns are a few of many Triassic genera which give a modern aspect to the earlier Mesozoic floras.

Another distinguishing feature of the later Triassic floras is the abundance of the Cycadophyta as illustrated by such genera as *Sphenozamites* with its handsome fronds bearing two rows of large truncate segments, *Pterophyllum* and *Pseudoctenis* with fronds similar to those of several existing cycads in the form of the leaflets. It must be remembered that the term Cycadophyta is used in a comprehensive sense embracing not only the living cycads, represented by a comparatively small number of species and genera for the most part tropical in range, but also an extinct group, the Bennettitales. The Bennettitales reached their maximum development in the Jurassic period and in the early days of the Cretaceous period when they were represented by a large number of types: in the form and structure of the stem and in their large palm-like leaves many of them must have borne a striking resemblance to modern cycads, but in the structure of the reproductive organs they differed in many characters from all existing cycads (see p. 86). The point which concerns us at the

moment is that the much greater wealth of cycadean plants in the later Triassic floras than in the earlier floras of the same period prepares us for their further increase in Rhaetic and Jurassic floras. Similarly the occurrence in some Triassic beds of the genus *Thinnfeldia* (fig. 4), which is probably a pteridosperm, characterized by fern-like fronds with leathery leaflets, is another example of the appearance of a new type which played a conspicuous part in Triassic, Rhaetic and Jurassic floras in almost all regions of the world.

The abundance in Upper Triassic floras of large-leaved species of the class Ginkgoales is a noteworthy character; the genus *Baiera* represented by large wedge-shaped leaves cut into linear segments and, in the more typical species, without a leaf-stalk, though already in existence in the Palaeozoic era began to play a prominent rôle in the vegetation of the Keuper stage; it persisted through the Rhaetic and Jurassic periods and survived into the Cretaceous.

Among other gymnosperms reference may be made to *Podozamites* (fig. 3), a tree with leaves similar to those of species of the living conifer *Agathis*, but distinguished from all recent genera by bearing its short, fertile, seed-bearing leaves in loose catkin-like clusters. *Podozamites* is an example of a genus which began its career in the Triassic period and became a cosmopolitan and abundant plant in Rhaetic and Jurassic floras. Our knowledge of the conifers is scanty; *Voltzia* survived from the early Triassic floras and with it some other members of the group which, through lack of material, cannot be closely compared with modern types.

In illustration of the salient features of the Triassic vegetation of Gondwanaland a brief reference is made to the plant-beds of South Africa. Sedimentary strata included in the Stormberg series have yielded a flora which shows many points of contact with the floras of the northern hemisphere. *Voltzia*, *Baiera*, *Pterophyllum*, *Pseudoctenis*, *Thinnfeldia*, *Schizoneura*, *Neocalamites*, genera of true ferns and plants with fern-like fronds occur with *Glossopteris* and other genera peculiar to southern Triassic floras. One of the most remarkable constituents of the South African vegetation is the genus *Rhexoxylon* founded on petrified wood; this was at first believed to be allied to a Palaeozoic group of gymnosperms, the Medulloseae, but an examination of additional specimens led J. Walton to compare it with certain species of *Dadoxylon*, a genus of conifers. The stem of *Rhexoxylon* reached a length of several metres and a diameter of 25cm.; it is characterized by a large pith with secretory ducts and some scattered vascular bundles, but more especially by the unusual arrangement of the wood, which was divided into wedge-shaped masses separated by bands of softer tissue and bears a very striking resemblance to the structure of some Dicotyledonous climbers in the tropical forests of the present day. *Rhexoxylon* is recorded from Triassic and probably Rhaetic beds in South Africa, and from the Antarctic continent. Nothing is known of the leaves or reproductive organs; the most interesting feature is the close agreement in the structure of the stem with that of certain living plants belonging to an entirely different section of the vegetable kingdom.

From a comparison of the fossil plants obtained from South Africa, India, Australia and South America it has been established that in its main features the Triassic vegetation of Gondwanaland was fairly uniform; many of the genera are common to both hemispheres and the distinction between the northern and southern continents was less obvious than in the latter part of the Palaeozoic era.

**Rhaetic Floras.**—The Rhaetic floras, richer than those of the Keuper series, are preserved in deposits formed for the most part in the estuaries of rivers and represented in many widely separated regions. Between the late Triassic plants and those furnished by the overlying Rhaetic rocks the difference is comparatively slight; there is a greater wealth of material in the Rhaetic beds and, though new forms occur, the general facies is similar to that of the Keuper vegetation. A rich Rhaetic flora has been described from Tongking; another equally rich flora has left abundant remains in southern Sweden and more recently a no less luxuriant flora has been described from Rhaetic rocks in the Scoresby



Sound district in Greenland (Harris, 1926). Collections of the same geological age have been made from central Europe and from many other regions. Though it is not easy precisely to correlate the rocks of Gondwanaland with those in the northern hemisphere, we know that in its broader features the vegetation which flourished south of the Tethys sea agreed with that of the rest of the world. This statement is not intended to give the impression of a vegetation unaffected by differences in climate; there were undoubtedly regional peculiarities, but there were many genera which appear to have had a remarkably wide geographical range. In the Rhaetic flora of Tongking *Glossopteris* is a connecting link with the Permo-Carboniferous vegetation of Gondwanaland, and the recently re-recorded occurrence of the genus as far north as Lat. 70° N. in Greenland demonstrates clearly its capacity as a traveller. In the Tongking flora we find also *Equisetites* and *Neocalamites* represented by species closely allied to northern forms. Among the ferns are many splendid examples of *Dictyophyllum* and *Clathropteris*, suggestive of the fronds of Malayan species of *Dipteris* (fig. 5, the smaller fronds); also of the *Osmunda* family. The various forms of simple *Taeniopteris* leaves recalling those of the hart's tongue (*Scolopendrium*), may be the foliage of Cycadophyta and not true ferns. *Pterophyllum* seems to have been one of the most conspicuous members of the Cycadophyta, a class represented by other genera such as *Ptilophyllum* and *Otozamites*. The fronds known as *Ptilophyllum* are characterized by two rows of linear segments giving them an appearance similar to that of the leaves of the Mexican cycad *Dioon*: *Otozamites* fronds are distinguished by the eared base of the segments which are occasionally relatively broad. Species of the cosmopolitan *Podozamites* also occur. It is pointed out by Dr. du Toit, in his recent account of the older Mesozoic floras of South Africa, that while the Tongking flora contained several plants specifically identical with South African and Australian forms, the absence in the Far Eastern vegetation of *Ginkgoites*, *Thinnfeldia* and other common Rhaetic genera is an interesting feature.

As we analyse more carefully the Triassic-Rhaetic floras of the world we shall no doubt find evidence of regional differences comparable, though less pronounced, to those in the vegetation at the present day. The close correspondence between the floras of east Greenland and the province of Scania (southern Sweden) is a remarkable fact. When we think of the enormous difference between the present north Temperate vegetation of Sweden and the treeless and stunted Arctic flora it is very difficult to understand the extraordinary resemblance presented by the two fossil floras, not only in the number and variety of the plants but also in the size of the vegetative organs. It is very unlikely, so astronomers tell us, that the earth's axis has changed its position, or at least to an extent that would make any appreciable difference to climatic conditions during that portion of geological history with which we are concerned. A possible explanation is offered by the Wegener hypothesis; in the Rhaetic period Greenland may have occupied a position relative to Europe and to the north pole different from that which it occupies to-day. There seems to be no satisfactory solution of this and other climatic problems raised by palaeobotanical researches if we reject, as we probably must, the suggestion that the axis of the earth has altered its position, and if we follow some of Wegener's critics and reject also the hypothesis which assumes changes in the relative positions of portions of the earth's crust.

There are few more attractive problems than those raised by the discovery of comparatively luxuriant floras in the Arctic regions. It is clearly impossible to make any definite statement of scientific value as to the temperature necessary for the existence of a vegetation composed of extinct species. We are apt to assume that a plant from Rhaetic or other strata, if it bears a resemblance to one which still exists, must have required for its normal development climatic or other conditions approximately the same as those prevailing in the localities of its modern representative. Such an assumption might be reasonable if based on a comparison of an assemblage of many extinct and recent forms, but it must be remembered that living plants closely related to

one another are often able to exist in places with sharply contrasted temperatures. Making due allowance for the adaptability of closely allied species to widely different conditions, and admitting the danger of applying knowledge derived from observations on living plants to species which became extinct many million years ago, there remains the problem of accounting for the occurrence in southern Sweden and in eastern Greenland of floras that are in general terms identical.

What then are the salient features of the Arctic Rhaetic flora? Among the Equisetales are species of *Neocalamites* in no way inferior to those from Queensland, Tongking, South Africa and elsewhere. The discovery of a large Lycopodiaceous cone, *Lycostrobus Scotti*, in the Rhaetic flora of Sweden and the subsequent recognition of spores in the Greenland beds, which are almost certainly referable to *Lycostrobus*, affords one of the few instances of the survival into the Rhaetic period of a plant bearing a striking resemblance to the *Lepidodendra* of the Carboniferous forests. Ferns are represented by large fronds of the genus *Todites*, that are so named from their likeness in form and in the structure of the spore-capsules (sporangia) to the living osmundaceous fern *Todea barbara* of South Africa and New Zealand, and by species with fronds of the type designated as *Cladophlebis* a genus that was widespread also in the Jurassic period. The occurrence in Greenland of pieces of fronds hardly distinguishable from a species of *Gleichenites* described from the Lower Jurassic flora of Franconia in Germany, affords some evidence of the existence in the Arctic flora of a member of a family that is now very widely spread in the Tropics and in the Cretaceous period was particularly prominent in the vegetation of western Greenland. Among other ferns are *Matonidium*, similar in habit to the living *Matonia* (fig. 5), *Laccopteris*, *Dictyophyllum*, and *Hausmannia*, genera agreeing in habit and in the structure of the sporangia with what has been called by F. O. Bower the *Matonia-Dipteris* alliance.

One of the most clearly established facts in the history of ferns is the striking contrast between the present restricted geographical range of the two Malayan genera *Matonia* and *Dipteris* and the almost world-wide range of Mesozoic ferns, described under several generic names, which are believed on good evidence to be nearly related to one or other of these plants. The two living genera, figured by A. R. Wallace (fig. 5) side by side on Mt. Ophir in the Malay Peninsula, may be regarded as relics of a remote past, survivors of a line of ancient lineage, which after wandering over the world from Arctic lands to the far south and east persist as impressive links with a vanished world.

Reference has already been made to the genus *Thinnfeldia*; the fronds of this plant and those of a somewhat similar genus *Lepidopteris* are widely scattered Rhaetic types. *Lepidopteris*, bearing small, thick leaflets with rounded tips, is one of the Rhaetic genera which though fern-like in habit is probably a Pteridosperm: it is recorded from Greenland, Sweden, Germany, Poland and Madagascar. *Thinnfeldia* and *Lepidopteris* differ from ferns in the more leathery texture of the leaflets, which are more resistant than those of ferns to certain chemical reagents, and by the absence of any sporangia of the typical filicean type. Both may be Pteridosperms, anachronisms in the Mesozoic floras.

As we pass from Triassic to Rhaetic floras cycadean plants increase in number and diversity of habit. Our knowledge of these plants is based mainly on external form of the fronds, some simple and undivided, others with a lamina dissected into broad, equal or unequal segments (for example, *Nilssonia*) or, as in the leaves of modern cycads, with separate leaflets attached to a strong rachis (e.g., *Zamites*, fig. 6, and *Otozamites*). It has, however, been possible to supplement the distinguishing characters afforded by external differences by the more trustworthy criteria furnished by the microscopical structure of the epidermal layers. We know little of the reproductive organs of many of the Mesozoic Cycadophyta, but in a few instances it has been possible to make out the characters of both the male and female organs. One example may be quoted: Prof. Nathorst described under the name *Wielandiella* regularly forking stems bearing in the angles bud-like shoots consisting of a short and thick axis



covered with a mosaic of two kinds of appendages, the greater number sterile, slender scales (interseminal scales) with slightly expanded flat tops surrounding similar appendages which were fertile and bore each a small terminal seed. These seed-bearing and sterile scales may be regarded as modified leaves. From the base of the fertile axis "flower" were given off short modified leaves bearing sporangia containing microspores (pollen-grains). The whole fertile shoot was surrounded by linear leaves (bracts). On the forked stem were simple foliage leaves similar in shape to small fronds of a hart's tongue fern but with the blade divided into segments. The plants must have resembled a shrubby *Magnolia*, the fertile shoots being superficially comparable to the flower but differing from all existing flowers in the nature of the female organs. *Wielandiella* agrees in the general plan of its "flowers" with the genera *Cycadeoidea* and *Williamsonia*, that came into prominence in the Jurassic period and flourished in the early days of the Cretaceous period. The two latter genera agreed in form and to a large extent in structure with living cycads: *Wielandiella* on the other hand differed widely both from the two extinct genera and from all recent cycads in the much more slender and dichotomously branched stem.

Among other genera met with in Rhaetic floras in many parts of the world are *Sagenopteris* and *Podozamites*. *Sagenopteris* is represented by leaves with a few (three to six) narrow oval or elliptical leaflets springing like the fingers of a hand from a single stalk and resembling *Glossopteris* in the network of veins. The genus has often been compared, on account of leaf resemblance, with the water fern *Marsilia*, but Dr. Thomas has made out a good case in favour of referring to *Sagenopteris* two different kinds of fertile shoots, or catkins, bearing spherical fruits (fig. 8A) or groups of pollen-sacs. The female shoots, described by him as species of *Gristhorpia* and *Caytonia*, consist of an axis bearing two rows of short branches each of which carries an apical case containing seeds which is compared with the carpel (pistil) of a flowering plant (fig. 8A-C). These "carpels" differ from those of modern plants in being modified leaflets, and not formed from complete leaves. The male shoots, referred to the genus *Antholithus*, are of similar form and their branches bear clusters of four-lobed stamens containing winged pollen-grains. The fruits, first described from the Jurassic rocks of Yorkshire, contain closely packed seeds (fig. 8C); on the surface of the wall near the attachment of the fruit to its stalk is a stigmatic lip (fig. 8B) for reception of the pollen. Dr. Thomas instituted a new class, the Caytoniales (from a locality near Scarborough where the fossils were found) for these supposed primitive Angiosperms. Rhaetic and Jurassic floras have long been known to be rich in gymnosperms, particularly in Cycadophyta, but with the exception of a single leaf, which if it had been found in Cretaceous or Tertiary beds would have been referred to a Dicotyledonous plant, no evidence of the existence of the great class Angiospermae (flowering plants) had been furnished by the earlier Mesozoic floras. One of the attributes of angiosperms is the production of ovules, which after fertilization become seeds, in a closed vessel or ovary, a character implied in the name of the class (seeds contained in a case), in contrast to the naked seeds of conifers and cycads. It is at least certain that the Caytoniales which are represented in Rhaetic as well as in Jurassic rocks, are the most satisfactory examples so far discovered of extinct plants with a definitely angiospermous attribute. The abundance of angiosperms in some of the older Cretaceous floras and the rapidity with which they wandered over the world during the earlier stages of the Cretaceous period suggest that they must have been evolved long before they came to occupy the premier position in the vegetable kingdom. The primitive types of angiosperms probably differed widely in habit from those with which we are now familiar. *Sagenopteris* may be a pioneer of the present ruling dynasty, which having passed slowly through the earlier stages of evolution reached its full vigour in the early days of the Cretaceous period.

Conifers, though less prominent than Cycadophyta and ferns, were fairly numerous in Rhaetic floras; some were closely allied to living members of the *Araucaria* family; others such as *Stachytaxus* with its yew-like foliage differed considerably in the fertile

shoots from all recent species. Species of *Baiera*, *Ginkgoites* and other members of the Ginkgoales with leaves similar in form and in the structure of the epidermal layer to the "living fossil" *Ginkgo biloba*, are among the most abundant and widely distributed Rhaetic plants.

### JURASSIC FLORAS

Samples of the vegetation prevalent in Jurassic times are scattered through the rocks from the far north in Franz Josef Land and Alaska to north and central Europe, Siberia, India, Japan, North America, and in Graham Land on the borders of Antarctica. One of the best known floras of the Middle Jurassic period is that preserved in the upraised sediments of estuaries which form the moors and cliffs of east Yorkshire. In its main characters the Jurassic vegetation carried on the tradition which began in the latter part of the Triassic period and was further developed in the Rhaetic period. Many Rhaetic genera persisted; some new types were evolved, and a comparative study has shown that while the Rhaetic facies in its broad features was maintained there are certain characters by which Jurassic floras can usually be recognized. A brief comparison with the present vegetation of the fern-covered river-banks and the shrubs and trees on the deltas in the area that is now traversed by the Yorkshire cliffs, from north of Whitby to south of Scarborough, may enable us to realize the more striking contrasts between the present and the past. Then as now there were horsetails (*Equisetum*) forming miniature forests on the swampy ground: the plants were more robust and taller than their modern descendants, though they were smaller than their Triassic forebears. The reign of *Schizoneura* and *Neocalamites* was almost over: among the commoner plants were many which no longer occur in Europe: a botanist wandering over the deltas would be reminded of lands south of the equator: ferns such as *Dictyophyllum* and *Matonidium* would recall *Dipteris* and *Matonia*; he would also find species belonging to the Schizaeaceae, Gleicheniaceae, Marattiaceae, and Cyatheaceae, families no longer represented in the British flora and most abundant in warmer, southern lands. He would note the prevalence of species, some of them unfamiliar in the architecture of the fronds, agreeing in the structure of the spore-capsules (sporangia) with the royal fern (*Osmunda regalis*). He would also discover clumps of *Thinnfeldia* probably occupying drier ground, the fern-like fronds characterized by their stiffer leaflets without sporangia of the normal fern type. Passing to the taller shrubs and trees he would be struck by the abundance of stems bearing crowns of fronds of diverse form resembling in a greater or less degree the sago palms (cycads) of the tropics. On closer inspection he would find that the cycadean plants bore shoots similar in shape to the flower heads of the globe artichoke (*Cynara*), some of them unisexual, others with male and female organs on a single axis instead of the male and female cones of modern cycads. The great majority of these cycadean plants belonged to the Bennettitales, a group that has long been extinct, and not to the cycads in the narrow sense. Most of them were constructed on the ordinary cycad plan as regards the stem, but the type represented in the Rhaetic floras by *Wielandiella* persisted under a slightly different form into the Jurassic period. This aberrant Jurassic type was described by Dr. Thomas as *Williamsoniella*; it had a comparatively slender and forked stem bearing scattered leaves (*Taeniopteris*) more fern-like than cycadean in form, and in the angles of the forked branches bisexual "flowers" resembling those of *Wielandiella*. He would probably look in vain for oaks, elms, sycamores, the ash, alder, and other broad-leaved trees, though he might discover some plants which would puzzle him by the association of a strange type of foliage with flowers distantly related to those of some modern angiosperms. He would see cone-bearing trees reminding him of the Norfolk Island pine (*Araucaria excelsa*), trees with shoots like those of cypresses, the incense cedar of America (*Libocedrus*), and the Arbor vitae (*Thuja*); some with two-ranked leaves recalling the yews, the giant redwood of California (*Sequoia sempervirens*) and other conifers. The conifers as a whole would seem familiar, though the association in the North Temperate region of types that are now widely scattered in



warmer countries would afford an interesting topic of speculation on the vagaries of plant-dispersal. He would be surprised to find many trees exhibiting clear signs of relationship to the maidenhair tree (*Ginkgo*). From his knowledge of present-day vegetation he would have difficulty in assigning to their position in the plant-world such genera as *Sagenopteris*, *Thinnfeldia* and other legacies from older floras.

There were frequent though comparatively slight oscillations of the earth's crust in the course of the Jurassic period which are registered in the varying nature of the sedimentary rocks—series of beds rich in the shells of marine creatures associated with deposits formed in estuaries and lakes. The period is subdivided into stages grouped as Lower, Middle, and Upper Jurassic. A considerable interval of time separated the stages represented by the plant-bearing beds of Lower Jurassic age, such as occur in England on the coast of Dorset, from Upper Jurassic dirt beds (old surface-soils) near Lulworth cove in the same county. Beds intermediate in age are exposed on the Yorkshire coast. It is unnecessary to follow the changes in the rise and fall of individual species from the earlier to the later stages of the period; there were differences in detail, but the main features of the vegetation so far as we know remained fairly constant. Ferns, Cycadophyta, Ginkgoales and conifers continued to be the ruling dynasties from the Rhaetic through the Jurassic period.

**Cretaceous Floras.**—In the south of England and in some other parts of the world there is no sharp line of division between the last phase of the Jurassic period and the dawn of the Cretaceous period. In the Weald district of Kent and Sussex, in northern France, Germany and Belgium a series of fresh-water beds contains records of a time when rivers carried into a large lake logs of wood, twigs, leaves, and other samples of the vegetation which grew on the adjacent land. From the relics of this flora preserved in the cliffs at Ecclesbourne, near Hastings, on the south coast of England, and at other localities in western Europe it is possible to form a picture of the plant-world at the beginning of the Cretaceous period. The differences between this Wealden flora in northern Europe and the preceding Jurassic floras are comparatively slight: a few new forms are met with, for example a plant known as *Weichselia Mantelli* usually regarded as a fern with spreading fronds bearing small and thick leaflets; another fern *Orychiopsis psilotoides*, probably allied to the living genus *Orychium*, a member of the Polypodiaceae which is represented in the Far East and in other regions; also a fern of peculiar habit referred to the genus *Tempskya*, which may be a member of the Schizaeaceae, recorded from several European localities and from Montana; species of conifers agreeing in the needle-like leaves and in the cones with members of the family Abietineae which includes pines, firs, cedars, larches and other genera. The genus *Sagenopteris*, though not yet extinct, was much less in evidence in early Cretaceous than in Jurassic floras. In the Wealden vegetation of northern Europe there were no trees, so far as is known, other than conifers. The vegetation had still the Jurassic facies at least in the main. Reference has already been made to the structure of the fertile shoots of the Rhaetic genus *Wielandiella* and the Jurassic *Williamsoniella*, two examples of the extinct Bennettiales which in their comparatively slender, forked stems differ widely from all existing cycads.

One of the outstanding features of the early Cretaceous floras is the abundance of cycadean plants, a feature also of Jurassic vegetation. Most of the stems are of the type known as *Cycadeoidea*; the splendid specimen (fig. 9) from Upper Jurassic rocks of southern England, *Cycadeoidea gigantea*, agrees closely with stems of some modern cycads in its bulky form and in the closely packed persistent bases of old leaf-stalks which give a characteristic appearance to the plant. This species differs from most examples in the absence of fertile branches. The first typical representative of the genus is one described by Carruthers from Lower Cretaceous beds in the Isle of Wight named *Bennettites Gibsonianus* and now included in *Cycadeoidea*. Embedded among the leaf-bases are several lateral branches bearing a terminal "flower" and numerous short, linear leaves. In this species the flowers appear to be unisexual and female. The discovery in

Dakota and in other districts in North America of hundreds of stems preserved in wonderful perfection supplied material which was described by Dr. Wieland in two well-illustrated volumes. Some of the stems are unbranched; others consist of several tuberous branches. A remarkable feature is the extraordinary abundance of fertile shoots on a single stem. The flowers are usually bisexual, some bearing male and female organs which were apparently functional; others with female organs only and with scars showing the former presence of male organs. A fertile branch ends in a depressed dome or in a tapered cone (fig. 10A) covered with two kinds of appendages, fertile ovule-bearing or seed-scales, each surrounded by a rosette of sterile inter-seminal scales with swollen, flat tips (fig. 10B) forming a protective layer over the whole "fruit." Below the female portion was a circle of 10–20 pinnately branched stamens bearing rows of compound sporangia (pollen-sacs) with numerous pollen-grains. The stamens were at first infolded round the flower-axis; after expanding and shedding the pollen they fell off. The fertile branch bore numerous hairy bracts, which surrounded a conical axis, bearing short female organs (ovuliferous scales) and interseminal scales enclosed by a series of infolded leaves (stamens) bearing rows of compound sporangia (pollen-sacs). The seeds contained an embryo with two cotyledons. The male organs may be compared on a small scale with the fertile leaves of modern ferns of the family Marattiaceae; while the female organs are of a type that is peculiar to the Bennettiales (e.g., *Wielandiella*, *Williamsoniella*, *Williamsonia*, *Cycadeoidea*). The largest example of a flower so far recorded is one described by Dr. Marie Stopes from Lower Cretaceous beds in the Isle of Wight which produced thousands of small seeds on a single "fruit." *Cycadeoidea* in its reproductive apparatus differs fundamentally from existing cycads though in the form and structure of the stem it is similar to them. It has been suggested that the general resemblance of the bisexual flowers to those of a magnolia may be an expression of actual affinity and that the angiosperms, which replaced the Cycadophyta as the ruling dynasty in the early days of the Cretaceous period may be connected with them by descent. The chief difficulty in the way of accepting this view is the lack in the flowers of the Bennettiales of any structure definitely comparable with an ovary. A few leaves discovered in strata on the Atlantic border of the United States of America, in the so-called Potomac series the lowest members of which are approximately equivalent to the English Wealden series, bear some resemblance to those of certain modern flowering plants; but their precise nature is uncertain. On the other hand Lower Cretaceous beds along a strip of the west Greenland coast on Disko island, on the coast of the adjacent mainland and on Upernivik island (Lat. 71° N.) have yielded several Wealden species. A species of *Ginkgoites*, ferns allied to *Matonia* and *Dipteris*, several forms of *Gleichenites*, closely allied to tropical and sub-tropical *Gleichenias* and to fossil members of the family recorded from Jurassic rocks, also some Wealden species of gymnosperms, associated with many leaves practically identical in form and venation with those of living flowering plants. Plane trees, magnolias, oaks, also leaves described as *Dalbergites* because of their striking resemblance to the foliage of the tropical genus *Dalbergia*, a member of the Leguminosae. It is significant that in no other part of the world do we find a greater abundance and variety of angiosperms preserved side by side with ferns and gymnosperms, which appear to be specifically indistinguishable from Wealden species from northern Europe, North America and many other parts of the world. It would seem, therefore, that many of the broad-leaved trees may have had their origin in the early days of the Cretaceous period on an Arctic continent whence in later times they spread farther and farther towards the south.

It is worth while to consider in rather more detail the nature of the vegetation which flourished in Greenland in the earlier stage of the Cretaceous period. We have already commented on the luxuriance of the Rhaetic flora of Scoresby Sound in east Greenland; the Lower Cretaceous flora has been partially reconstructed from specimens obtained from beds on approximately the same latitude (Lat. 70–71° N.) on the opposite coast. Another question



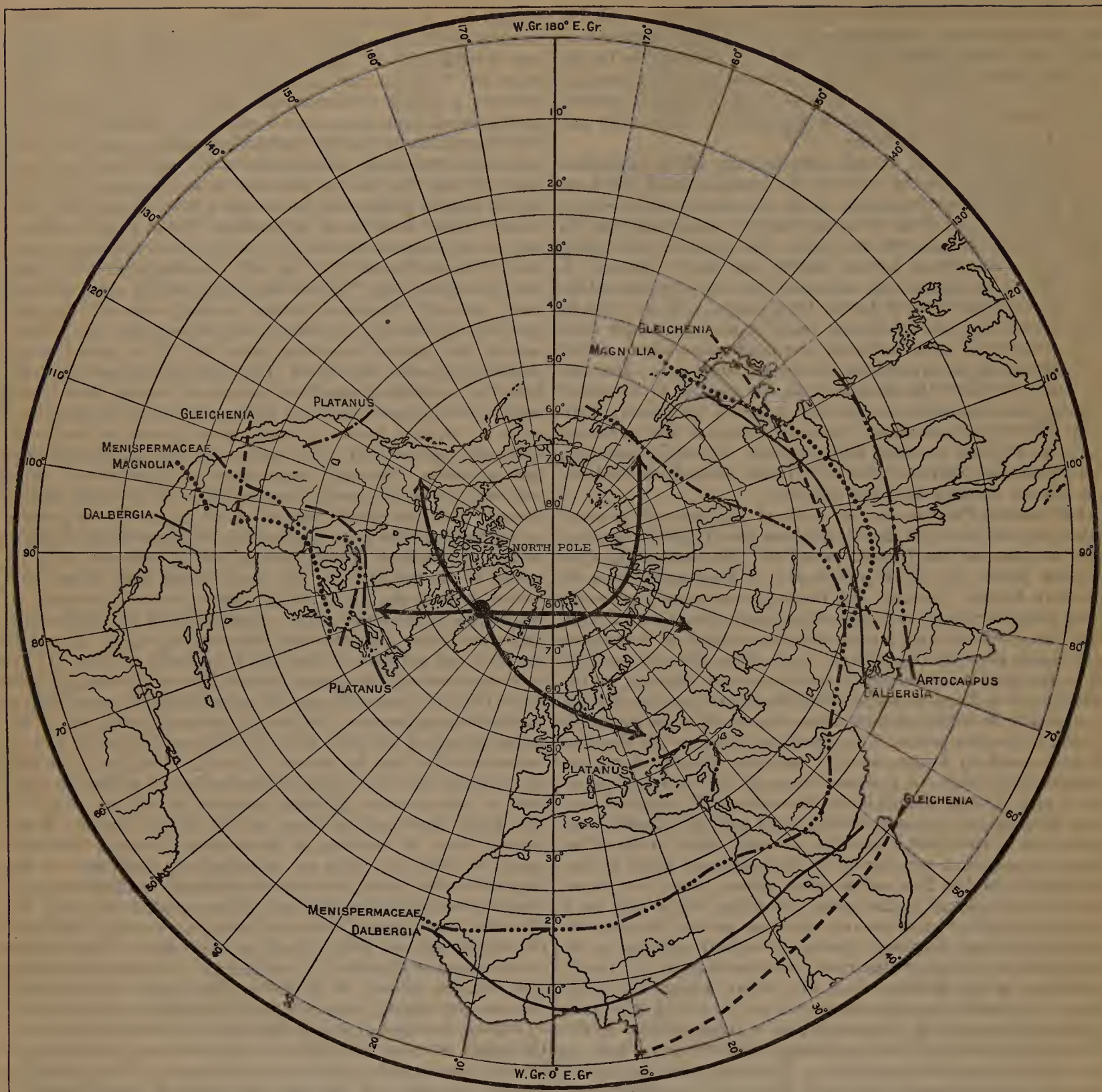


FIG. 12.—MAP OF THE NORTHERN HEMISPHERE SHOWING, ON THE WEST COAST OF GREENLAND, THE DISTRICT WHERE A RICH LOWER CRETACEOUS FLORA HAS BEEN FOUND

The arrows indicate a Southern Migration of Arctic Cretaceous plants. The present northern limits of families and genera represented in the Greenland Cretaceous flora are shown by the various lines

of great importance and of no little difficulty is the apparently sudden transformation of the older Mesozoic vegetation, in which flowering plants played little or no part, into what we may call a vegetation that is entirely modern in its dominant characters. The only indication in Rhaetic and Jurassic floras of plants foreshadowing angiosperms in the nature of their reproductive organs is furnished by the Caytoniales. From Lower Cretaceous rocks in England above the Wealden series Dr. Marie Stopes described some highly specialized types of dicotyledonous wood which cannot be regarded as primitive. It is therefore certain that angiosperms had reached an advanced state of development at a comparatively early stage in the Cretaceous period.

The salient features of the west Greenland flora may be briefly summarised as follows: Species of *Gleichenites* were the chief representatives of the ferns; they agree closely in the forking of the frond axis, in the structure of the spore-capsules, and in the

anatomy of the leaf-stalk with existing species of *Gleichenia*. Among other ferns are *Laccopteris*, a genus that in the form of the fronds and in the structure of the sporangia bears a striking likeness to *Matonia*; *Hausmannia* closely allied to *Dipteris*; species of *Sphenopteris* and *Cladophlebis* which have not as yet been assigned to a definite position in relation to living species. The Cycadophyta are represented by plants bearing leaves having the characters of *Pseudocycas*, *Ptilophyllum* and *Otozamites* genera which played a prominent part in Jurassic floras. The fronds known as *Ptilophyllum* are characterized by two rows of linear segments giving them an appearance similar to that of the Mexican cycad *Dioon*; *Otozamites* fronds are distinguished by the eared base of the segments which are occasionally relatively broad. Trees with leaves like those of *Ginkgo* were abundant in the Arctic forests and with them were other members of the Ginkgoales. Conifers were represented by species believed to be akin



to *Araucaria* and *Agathis* of the southern hemisphere, by members of the cypress family, relatives of the sequoias of California, at least one species of Abietineae, and by several conifers with leaves resembling in structure those of the umbrella pine (*Sciadopitys*) of Japan. With these were associated several species of dicotyledons surprisingly modern in the pattern of the foliage: in addition to the genera previously mentioned special attention is drawn to *Artocarpus*, the tropical bread-fruit tree. The occurrence of leaves agreeing closely in venation with those of the cinnamon tree (*Cinnamomum*) and of members of the Menispermaceae, a family of flowering plants that is now characteristic of tropical and warm temperate countries, affords further evidence of unusual climatic conditions in the Arctic regions (Map, fig. 12). We cannot believe that the evolution of the flowering plants was a sudden event. The oldest known angiosperms so far discovered must be the descendants of a line of ancestors stretching far back into the earlier stages of the Mesozoic era.

**Conclusion.**—A comparative study of the records of plant-life shows that the character of the vegetation was fundamentally changed during the later stages of the Palaeozoic era; a few of the older types survived, but most of the plants which flourished in the Coal age disappeared. By degrees as the Triassic period advanced, ferns of modern aspect increased rapidly in number and displaced the Pteridosperms from their position of dominance. The seed-bearing fern-like plants were by no means extinguished but they were overshadowed by the gradual rise to power of the Cycadophyta, the Ginkgoales, and other groups. The next great change in the plant-world was at the end of the Jurassic period and at the beginning of the Cretaceous period when the present dominant class, the angiosperms, began to assert its ascendancy and the floras became modified "as by a new creation." It is impossible to follow in detail the progress of evolution during the Cretaceous period as a whole. The important point is that at the beginning of the period flowering plants were small in number or entirely absent; this is the conclusion based on the very incomplete data at present available. In the Lower Cretaceous floras of Greenland, North America, Bohemia and Sakhalin Island in which dicotyledons first appear in quantity there were also several representatives of gymnosperms and ferns which had survived from the Jurassic period. As we ascend to the higher divisions of the Cretaceous period the floras become more modern and the chief differences between them and those of our own day are geographical rather than botanical. The floras of North America and Europe, for example, agree much more closely with present-day floras in sub-tropical or even tropical lands than with the plant associations which now occupy the territory where the fossils have been found. The problem of climatic change raised by the Cretaceous vegetation of Greenland has still to be solved. On the accompanying map (fig. 12) the northern limit of distribution of some of the families and genera is roughly shown. If we assume that the Greenland Cretaceous species grew under conditions similar to those which govern the life of their present-day relatives, it follows that the climate must have been at least as warm as that in the Mediterranean region at the present time. It is certain that the Cretaceous vegetation could not have endured the hardships imposed on the present Arctic floras; but it is by no means certain that extinct species of living genera could not have existed under conditions which would be fatal to their modern descendants. The past is in many respects the key to the present; but it is dangerous to carry this principle too far.

From the broken fragments of plants preserved in the sedimentary rocks of the Mesozoic periods we have been able to reconstruct a few of the links in the middle portion of the chain of life and to follow the varying fortunes of certain groups and families through successive ages. The history of the plant-world may be compared with that of human races; for a time one race holds sway over a widening territory unchecked by serious competitors until, with apparent suddenness, a more efficient stock asserts itself and the balance of power is disturbed. In the contrast between the vegetation of the Cretaceous period and that characteristic of the earlier stages of the Mesozoic era we have one of the most impressive illustrations of the revolutionary aspect

of evolution presented by the records of the rocks.

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### TERTIARY PLANTS

**Introduction.**—The great geological divisions into Primary, Secondary and Tertiary eras are based chiefly upon the observations of marine strata and marine organisms. The reason for this classification lies in the fact that oceans are more continuous than land, and sea organisms therefore present a more universal basis for classification than land organisms. But changes in land life do not always coincide with changes in marine life, and for this reason a different grouping of geological periods is better for the study of plants. The last great phase in the development of plant life is the coming in of flowering plants. Tertiary botany is chiefly concerned with the history of these; but for their origin we must go back to the Cretaceous.

With the advent of flowering plants the age of world-wide floras is left behind. From this time onwards plants are grouped into localized floras comparable with those of the present day.

**Mode of Occurrence of the Plants.**—Hardly ever has a whole fossil plant been found with its parts in association. Not uncommonly fruits containing seeds, and leaves attached to stems occur. Thus material available for the study of Tertiary plants is fragmentary. Most of the determinations are based on leaves, fruits and seeds, but there are notable exceptions. In the Baltic amber various delicate organs are preserved. Pollen has chiefly been studied from the Quaternary peat of northern Europe.

Tertiary and Quaternary plant deposits are formed in various ways. Sometimes the portions of the plants are embedded in the silts of ancient lakes, as in central France, Switzerland, and the



Rocky mountains; sometimes in the silts of rivers, as in the beds formed by the old Rhine; or sometimes in the brackish water silts of estuaries, as in the beds of the Hampshire (England) coast. Again plant deposits may be the accumulations of swamps, e.g., the brown coal of Germany; or of successive layers of vegetation occupying the same spot, like the peat of northern Europe. Yet again plants may be buried by volcanic ejecta, as has happened in Scotland, Ireland and central France. Or they may have become entangled in resin, as has happened in the case of the Baltic amber. It is from such scattered information, overlapping now in one place, now in another, that the history of Tertiary plant life in Europe is pieced together. Whatever the mode of origin, there are corresponding differences in the kind of matrix, in the parts of the plant preserved, and, generally, in the components of the floras.

Leaves usually occur in fine clay or tufa, and most frequently as mere impressions showing more or less clearly the form and nervation; but, in the case of coniferous and evergreen leaves, not infrequently part of the carbonized leaf itself is preserved covered by its tough cuticle. Delicate winged and pappus-bearing fruits and seeds also occur in fine clays. Other fruits and seeds, also wood, are found embedded in coarse material such as sandy clays, sands and loam, and in peat. Usually if carbonaceous substance is present, it is impregnated with mineral matter. If, as is common, this is iron pyrites, the close intermixture of hard pyrites with rotten carbonaceous matter makes it difficult to examine the objects by sectioning. Sometimes the carbonaceous substance is entirely replaced by silica or calcite, when sectioning becomes possible.

**Methods of Study.**—Different organs being differently preserved, each part of the plant requires a special method of study. Leaf impressions require no preliminary treatment beyond exposing any part concealed. When the leaf-blade is preserved, a fragment must be chipped off with a knife and, by treatment with nitric acid and chlorate of potash followed by ammonia, the cuticle can be isolated, mounted on a microscope slide, studied and photographed. Winged and pappus-bearing fruits and seeds must be studied in the same way. Other fruits and seeds are isolated by disintegrating the matrix. This may be done by boiling the seed-bearing material in a strong soda solution, or warming in a 10% solution of nitric acid over a water bath. The dissolved matrix is then strained off through sieves, leaving the fossils behind. These can be examined as free entities. In the investigation of pollen grains the material is boiled with a 10% solution of caustic potash. Wood, being large, is usually picked out of the matrix with a knife or other instrument, and, if possible, sectioned and studied microscopically.

The number of living species is so great, and the required knowledge so detailed, that rarely does a worker attempt more than one branch of the study. All workers have one initial need in common—as complete a collection as possible of those parts of the living plant they wish to study. Ideally, all living species should find place in the collection, and the material should be arranged so as best to suit the particular branch of study. The arrangement of public herbaria is usually not very suitable for palaeobotany. The reason lies in the method of classification of living plants. This is based principally on the arrangement of the floral organs, although other organs play a subsidiary part. In consequence all collections of dried plants, and all books dealing with classification, are arranged on this basis, and afford no ready key to the palaeobotanist, as they do to the botanist. For the former the organs he studies have always to be re-classified. All great herbaria provide abundant material for the study of leaves, but not for that of other organs. Fruits and seeds are badly represented, and there is great need for better collecting of these organs.

Either from collections or illustrations, the student must gather all possible material for comparison. But the living material is the most important. He must examine the fossil and living part in detail, using the microscope. Stress is laid on the comparison with living material, for sometimes palaeobotanists have been content to follow the easier course of comparing with previous

determinations only. But on the exact comparison with living plants depends our knowledge of the relation of fossil species to living ones.

**Scope of the Study of Tertiary Plants.**—Tertiary plants furnish some of the later chapters in the history of living plants, and of the world; the latest of all being found in the Quaternary. They give the most reliable information obtainable about the ancestors of the living forms; where they lived and what their various organs were like. That is to say, what changes in distribution and structure they have undergone, or, on the other hand, what stability they may show. They give also the best information obtainable as to past climate.

In the early stages of the period we can trace no living species, but some species are sufficiently close to living ones to be placed in living genera. Others which cannot be placed in living genera may yet be placed in living families. Nevertheless, until the close of the Tertiary period, plants constantly occur whose living relations have not been discovered. Whether this is because the plants have become extinct and left no link with the present, or because our knowledge of living plants is inadequate to trace their relations is difficult to tell. Probably both causes operate. It is certain, however, that old forms more remote from the living have yielded place to newer forms closer to the living; so that by the end of the Tertiary period (latest Pliocene) all known fossil floras are composed, almost exclusively, of living species, although the geographical distribution of these may have changed in the interval.

The study of a succession of floras in a given region, say western Europe, shows clearly that changes occur in their components from age to age. Further, that the components of the successive floras are related to those of living localized floras; now to a tropical, now to a warm-temperate flora, and so on.

But living plants are grouped into localized floras largely under the influence of climate. Adverse climatic conditions will kill developed, *i.e.*, rooted, plants. Whole species, or even genera would be killed out, were it not that plants have an inherent power of movement in their embryo stage—the seeding stage. If the members of a species can cast their seed beyond the range of the adverse conditions, that species may survive. If not, it must die. But for survival, the change of climate must not overtake its rate of travel, and there must be a suitable habitat within reach. That plants continually try to occupy fresh ground is shown by the rapidity with which they spring up on waste land (Krakatoa after the earthquake, Flanders during the war). That they fail to establish themselves, if the ground is already occupied by a healthy population, is shown by the rarity with which introduced plants are able to establish themselves among a native flora. It is largely by movement under changing climate that in process of time plants have been grouped into the existing local floras. Under a change from heat to cold the movement will be from higher to lower latitudes and from higher to lower altitudes. Under a change from cold to heat it will be in the reverse directions.

In considering the results which have accrued from the study of Tertiary plants, we propose to divide the subject under three heads belonging to the three great geographical regions in connection with which most of the work on Tertiary plants has been carried out. These regions are Europe, North America and the Arctic. The work on the Tertiary plants of all other parts of the world is, as yet, too scattered and too scanty to admit of treatment in a short article. Space does not permit of more than a general indication of the characters of the floras which succeeded one another in the three regions during the long Tertiary ages—probably some tens of millions of years. For fuller knowledge readers must consult the bibliography. Much of the older work needs revision, chiefly because the knowledge of the plants of the Far East—just those with which Tertiary plants are most closely allied—has increased so greatly during this century. In view of this increase in knowledge we illustrate the fossil floras of the various periods, where we can, by the latest work, provided the floras are large and their age well established. There is an additional advantage in so doing because the later works give references to the more important older works.



Typical Plant Deposits

Era	Age	Europe	America, <i>Am.</i> ; Arctic, <i>A</i>
Quaternary	Historic	Roman, Celtic, etc.	
	Neolithic	Peat of north Europe Dogger Bank peat, "Submerged Forests"	
	Palaolithic	Post-glacial, arctic Interglacial, warm Preglacial, arctic	Eastern Canada and eastern U.S.A.
Tertiary	Pliocene	Cromer Forest bed Mougoudo, Reuver	Citronelle, <i>Am.</i>
	Miocene	Brown Coal, Oeningen	Florissant, <i>Am.</i>
	Oligocene	Aix Bembridge, Baltic amber	Catahoula, <i>Am.</i> ; Alum Bluff, <i>Am.</i>
	Eocene	Hordle Bournemouth, London clay Sezanne, Gelinden	Green River, <i>Am.</i> Wilcox, <i>Am.</i> ; Spitzbergen, Greenland, <i>A.</i>
Secondary	Cretaceous	Plant beds of Saxony, Bohemia, Portugal	Laramie, <i>Am.</i> Dakota, <i>Am.</i> ; Potomac, <i>Am.</i> ; Kome, <i>A.</i>

## CRETACEOUS AND TERTIARY PLANTS OF EUROPE

The plant deposits of Europe, though numerous, are usually of limited extent and confined to small areas. When intercalated with marine beds the geological age may be clear; but frequently this does not happen, and then the age is doubtful, unless the deposits contain the remains of land animals, which sometimes help in correlation.

**Cretaceous.**—Flowering plants when they appear in Lower Cretaceous rocks, are represented, in Europe, by a few scattered specimens of very doubtful affinity; a few species represented by leaves, from Portugal, or wood, from England and so forth. As time progresses the remains become more frequent, but floras still retain their predominant Secondary character.

By the Upper Cretaceous, flowering plants begin to dominate, and from various parts of central Europe a considerable number of species have been recorded. In Bohemia, besides conifers and ferns, there occur many dicotyledons. *Credneria* is a genus of unknown affinity, but other plants have been referred to living genera. Such are *Myrica*, *Ficus*, *Quercus*, *Eucalyptus*, *Pisonia*, *Phillyrea*, *Rhus*, *Prunus*, *Bignonia*, *Laurus*, *Salix*, *Benthamia*. But without the evidence of fruits or flowers in support, it is difficult to believe that so many living genera existed.

After the Cretaceous there was an interval of unknown duration not represented by deposits in Europe. The Tertiary period which followed witnessed great changes in the physical geography of the continent. The great mountain-chains which span Eurasia were uplifted. As we shall see later this has had an enormous influence on the plant life of these regions ever since. In addition to mountain-building, there was also great volcanic activity in various parts. It is customary to divide the Tertiary into four periods: Eocene, Oligocene, Miocene, Pliocene.

**Eocene.**—The earliest Eocene, the Paleocene, is not represented in Britain, but is found on the Continent in the north-east of France, and in Belgium. The flora is still close to that of the

Upper Cretaceous, and indicates similar warm-temperate or sub-tropical conditions. Count G. de Saporta recorded from Gelinden, near Liège, species of oak, chestnut, laurel, cinnamon, camphor, *Litsea* and *Persea*; also members of the *Araliaceae*, *Menispermaceae*, *Celastraceae* and *Myrtaceae* families. From tufa formed by an ancient waterfall at Sezanne he recorded, besides a profusion of ferns, genera of *Lauraceae*, *Tiliaceae*, *Meliaceae*, *Sterculiaceae*; also *Symplocos*, *Artocarpus* (the bread-fruit), *Magnolia*, hazel, alder, willow, viburnum, cornel, fig, ivy and vine; but nearly all the European genera show an exotic character. From the Paleocene near Paris, Watelet recorded *Araucaria*, bamboo and palms.

Later in age are the Woolwich and Reading series of England from which a small but interesting flora suggests a rather more temperate climate than that which preceded or followed it. Leaves of plane are abundant, and among the plants recorded are *Robinia*, a palm, two figs and a laurel. C. von Ettingshausen and J. Starkie Gardner who worked on the beds, recorded two ferns, *Aneimia* and *Pteris*; and two gymnosperms, *Libocedrus*, related to the American *L. decurrens*, and a species of swamp cypress, *Taxodium europaeum*.

The Oldhaven beds which follow have yielded fig and cinnamon. None of these beds have as yet been fully investigated, and the evidence is too scanty for a correct inference as to climate.

The deposit next in age in England to which we must refer is the London Clay. It is the most important plant bed of Lower Eocene age in Europe. The fruits and seeds are very abundant and beautifully preserved. For more than two centuries they have attracted attention. In 1840 Dr. James Scott Bowerbank published an admirable study of some of them, but the work was never finished. His botanical knowledge was inadequate to allow him to determine the species. In 1879 Ettingshausen made a very hurried study of Bowerbank's material, and published a list of plants, but without any evidence to support his determinations. Critical examination of the same material by the writers, who are now engaged upon its study, proves that his work was faulty in the extreme and valueless. The work of revision is not completed, but it may be stated that, with the exception of a few representatives of sub-tropical genera, the affinity of all is tropical. Scarcely any of the genera have living representatives in Europe. The Nipa palm was one of the commonest species. In the present era it abounds on the margins of estuaries and lagoons in the tropics of east Asia. Other palms are common, and families wholly tropical find representation. It can scarcely be doubted that the climate of Britain was tropical, or nearly so, when the London Clay was deposited.

Similar evidence of tropical conditions comes from the Paris basin where, amongst other plants, numerous palms occur, including *Nipa*; *Ottelia*, a tropical water-plant of the Old World is also found. Saporta pointed out the further evidence for tropical conditions shown by the scarcity of caducous leaves, an absence which indicates the non-occurrence of seasonal changes. The middle Eocene of the Bournemouth beds (Hampshire) still shows something of a tropical character. The flora is as yet incompletely known, but Dr. Helena Bandulska has begun in connection with it, one of the few systematic studies of leaf-cuticles that has been made. Isolated cuticles have frequently been studied, but the systematic examination of living species is but begun. It may prove of great value. The Nipa palm (determined from fruits) flourished, also such tropical genera as *Aniba*, *Litsea* and *Neolitsea*; but somewhat cooler conditions may be evidenced by *Lindera* and *Nothofagus*. Gardner and Ettingshausen had previously recorded many ferns, also conifers including *Araucarites*.

We must draw attention to a curious and important fact. It has been noted that the flora of the London clay was exotic. All Tertiary floras continued to be so in a large degree until towards the end of the period. At first even the families were mainly exotic. Gradually European families came in, but the relationship of the genera was exotic. Then European genera began to appear, but the relationship of the species was exotic. Lastly, at the end of the Pliocene the whole flora was transformed to one of European species. Stated in another way: A flora of European relationship gradually replaced one of exotic relationship, which died out.



The relationship of the dying flora is very remarkable. In the Eocene it was more or less world-wide, but with a marked leaning to plants of the Far East. In floras later than the Eocene the relationship contracts. African affinities nearly disappear. Plants with relations in the Far East predominate. Next in order come North American and Mediterranean plants; then Australian, in spite of the fact that the Far East and America are so far, and the Mediterranean so near. Yet another way of stating the same fact is, that a type of flora which was gradually killed out in Europe, survived largely in the Far East and in America, and only in a very small degree in the Mediterranean. The parts of the Far East in which the living allies are found are Japan, China, Burma, further India, the Malay Peninsula, Malay Islands, Formosa, the Philippines; also Australia. In a general way as time passed the relationship passed northward from Malaya to Japan and China, and from the West Indies through the United States to Canada.

The upper Eocene of Hordle (Hampshire), the flora of which was described by M. E. J. Chandler, has yielded the conifers *Sequoia* (related to the red-wood) and pine. In addition there occur among flowering plants such tropical or sub-tropical genera as *Broussonetia*, *Chlorophora*, *Gordonia*, *Iodes*, *Menispermum*, *Natsiatum*, *Nipa*, *Orites*, *Phellodendron*, *Symplocos*, *Zanthoxylon*, and various vines. Among genera which now range into Europe are *Corydalis*, *Liquidambar*, *Styrax*, as well as the blackberry, elder and persimmon.

**Oligocene.**—In the succeeding Oligocene the change of flora is comparatively slow. The flora of the Bembridge beds (Hampshire) of Early Oligocene age, has lately been studied by E. M. Reid and M. E. J. Chandler. It contains a few tropical and sub-tropical genera such as *Epipremnum*, *Neolitsea*, *Phyllanthera*, *Radermachera*, *Tylophora*, but plants of a cooler range are also common; *Araucarites*, *Catalpa*, *Cinnamomum* (the cinnamon), *Engelhardtia*, *Incarvillea*, *Libocedrus*, *Sabal* (the palmetto), and numbers of genera which now have representation in Europe: Bulrush, bur-reed, pond-weeds, water-soldier, sedge, beech, oak, hornbeam, clematis, buttercup, poppy and *Acanthus*.

A flora of somewhat the same age is preserved in the Baltic amber. Reference has already been made to its mode of preservation. The plants include the amber-pine itself, from which the resin dripped, enclosing insects, leaves, twigs, wood, flowers, seeds and hairs. Many of the flowers closely resemble living forms. Among exotic genera are two palms *Phoenix* (the date-palm) and *Sabal*, *Clethra*, *Dalbergia*, *Deutzia*, *Ephedra*, *Hammamalis*, *Hibbertia*, *Magnolia*, *Stuartia*, *Trianthera* and *Ximenia*. Among European genera are *Daphne*, *Erodium*, *Geranium*, *Loranthus*, *Amarantus*, *Myrica*, *Smilax* and *Thesium*, besides oak, chestnut, beech, willow, polygonum, flax, maple, holly, buckthorn and wild-parsley. Probably this list needs revision. It will be noticed that a great number of these genera have not appeared in previous lists, and will not appear in later ones. The amber flora offers a good example of the selective process which accompanies different kinds of preservation.

One of the largest known fossil floras belongs to the Oligocene, that of Aix in Provence. It was determined by Saporta. It comes from the bed of an old lake. The lake itself long continued in existence, and the life around and within it suffered many vicissitudes whilst the region was convulsed by the earth movements and volcanic activity of the time, although no very great change took place in the flora from beginning to end. Some of the exotic families represented are *Bignoniaceae*, *Proteaceae* and *Sapotaceae*. Among exotic genera are *Aralia*, *Ailanthus*, *Bombax*, *Leucothoe*, *Magnolia*, *Sapindus*, *Sterculia*, *Zanthoxylon*. Several conifers and palms occur. *Lauraceae* are represented by cinnamons and camphors. Among European genera are *Arundo*, *Daphne*, *Smilax* and *Styrax*, bur-reed, bulrush, pond-weeds, alders, birch, oak, fig, poplar, willow, laurel, jasmine, olive, oleander and persimmon.

**Miocene.**—One of the earliest described and most famous of Tertiary floras was obtained from the silted up lake of Oeningen in Switzerland. From this Oswald Heer recorded hundreds of species. As his work needs revision, it will be better to take as a type of a Miocene flora the almost equally famous brown-coal of central Europe. Much recent work has been done on brown-coal

material derived from various localities by the late Dr. P. Menzel and Dr. R. Kräusel. Numerous conifers are found—*Sequoia*, *Taxodium*, and *Glyptostrobus*. The walnut family is strongly represented by American and Asiatic forms. Catkin-bearing trees are abundant. Among exotic genera are *Ampelopsis*, *Acanthopanax*, *Aralia*, *Cinnamomum*, *Elaeodendron*, *Lindera*, *Liquidambar*, *Magnolia*, *Persea*, *Symplocos*. Among European genera are *Cotoneaster*, *Paliurus*, *Sorbus*, *Spiraea*, *Trapa*, *Zizyphus*, plane, plum, hawthorn, blackberry, maple, *Euonymus*, holly buckthorn, lime and ash. In this flora are found forms so near the living as to be named as mere varieties. It must be remarked, however, that genera found in Europe are still often represented by species of exotic relationship.

The transition from Miocene to Pliocene is well represented in the old volcanic region of central France. E. M. Reid has described from fruits and seeds a late Miocene (or Mio-Pliocene) flora from Pont-de-Gail. Among alien genera are *Actinidia*, *Ametystia*, *Cleomella*, *Clerodendron*, *Ehretia*, *Epipremnum*, *Magnolia*, *Meliosma*, *Menispermum*, *Phellodendron*, *Polanisia*, *Symplocos*, *Trichosanthes*. All are of east Asian or American affinity. There are besides numbers of European genera which cannot here be named.

**Pliocene.**—The Lower Pliocene flora of Mougoudo (Cantal) is a little newer. It was examined by Prof. L. Laurent who recorded exotic *Lauraceae*, *Rhamnaceae* and *Malvaceae*, also *Zelkova*, *Abronia*, *Cissus*, *Grewia*, *Sterculia* and *Paulownia*.

The largest known Lower Pliocene flora is the Reuverian from the Dutch-Prussian border. It was studied by Prof. Laurent and by C. and E. M. Reid. Among exotics are *Actinidia*, *Araucaria*, *Aralia*, *Brasenia*, *Carya*, *Epipremnum*, *Euryale*, *Glyptostrobus*, *Karwinskia*, *Magnolia*, *Meliosma*, *Menispermum*, *Myrsine*, *Nelumbium*, *Nyssa*, *Phellodendron*, *Proserpinaca*, *Pseudolarix*, *Pterocarya*, *Sequoia* and *Zelkova*, besides many others. European genera are now numerous. Many living species occur, some of them European.

Similar evidence comes from the Rhone valley where M. l'abbé Georges Depape has recorded *Buettneria*, *Carya*, *Cinnamomum*, *Diospyros*, *Ginkgo*, *Glyptostrobus*, *Laurus*, *Liquidambar*, *Liriodendron*, *Oreodaphne*, *Persea*, *Pterocarya*, *Sapindus*, *Sassafras*, *Torreya*, *Zanthoxylon* and *Zelkova*, amongst exotic genera.

In the Middle Pliocene a great change occurred in the European flora. Very rapidly the old exotic plants disappeared and European plants took their places, almost with a rush. In the flora of Tegelen (Holland) but a few stragglers of the exotic genera remain: *Actinidia*, *Dulichium*, *Euryale*, *Magnolia*, *Phellodendron*, *Pilea* and *Pterocarya*. 84% of genera were European and 82% were represented by allies of European species. By the close of the Pliocene, i.e., the end of the Tertiary period, the Cromer forest-bed flora shows an almost exclusive European alliance. The old flora had gone.

#### CRETACEOUS AND TERTIARY PLANTS OF NORTH AMERICA

As distinguished from the European, the Tertiary flora of North America is characterized by the continuity of the great bulk of its elements from past to present, with only such changes as have attended evolution and plant migration within the continent; some of the more tropical forms having sought refuge in South America. When alien elements occur they show alliance with the Tertiary plants of Europe, or with the living plants of the Far East, and in a lesser degree with those of Africa and the Mediterranean. The alliance with the Far East continues to the present day, as Asa Gray and the late Prof. C. S. Sargent have pointed out. Hence the living flora of America is linked with the extinct Tertiary flora of Europe, and with the living flora of the Far East.

The Cretaceous and Tertiary plant deposits of North America present a magnificent series, often covering extensive areas. They may be divided into three chief groups: (1) The deposits of the southern and south-eastern coastal plains, a series studied by Prof. E. W. Berry. These show an ordered succession of strand floras of very similar character which lived under similar conditions, and are therefore closely comparable from age to age. They are dated by intercalated marine strata. (2) The deposits of the



eastern coastal plain; those of Cretaceous age being the most important. (3) The Rocky mountain group where a scattered series of continental deposits occurs, some of them having been formed, as were many in Europe, under the influence of mountain-building and volcanic action. The beds, like similarly isolated beds in Europe, are of somewhat doubtful age, but Cretaceous, Eocene and Miocene strata appear to be represented. The flora is of an inland type.

**Cretaceous.**—The Cretaceous witnessed in America, as in Europe, the passing of the flora of secondary type and the incoming of flowering plants. Conifers, cycads and ferns were still largely represented, but they diminished in number, and the older forms died out. The flowering plants of the Lower Cretaceous were markedly different from those of the present day. They are referable to living families, but only a few, such as fig and sassafras, to living genera. In the Upper Cretaceous, the flora became richer and more varied. It indicates a mild climate without seasonal changes. In the coastal beds of the south and from beds of similar age, which extend through Alabama and New Jersey and are found in West Greenland, a rich flora is found in which figs, willows and magnolias are predominant. From the Dakota Sandstone Leo Lesquereux described a considerable number of genera, among which may be mentioned *Aralia*, *Cinnamomum*, *Eucalyptus*, *Ficus*, *Ilex*, *Inga*, *Juglans*, *Laurus*, *Magnolia*, *Nyssa*, *Paliurus*, *Pinus*, *Populus*, *Quercus*, *Sassafras*, *Sequoia*, *Sterculia*, *Zizyphus*. These also indicate mild conditions.

The latest Cretaceous is found in the Laramie formation of the Rocky mountain group. The strata were laid down in a great inland sea which was gradually drained by the elevation and silting up of its bed. Coal seams indicate long persistent swamps and lagoons. In his study of the flora, the late Dr. F. H. Knowlton named ferns, the conifers *Dammara* and *Sequoia*, and, among flowering plants, *Anona*, *Ceanothus*, *Cercis*, *Hicoria*, *Magnolia*, *Nelumbium*, *Pistacia*, *Sabal*, *Zizyphus*, as well as species of walnut, willow, poplar, oak, bread-fruit, fig, ivy, holly; but many of the plants can only be referred to families; their more exact relationship being uncertain.

**Eocene.**—The Eocene saw a sudden development of modern types. Almost all the plants are closely allied to those which inhabit the warm regions of the earth. Even when genera range into cooler regions they are, in almost every case, represented in the tropics also. The largest Lower Eocene flora is the Wilcox flora described by Berry. Most of the plants are tropical or subtropical, a few are allied to temperate forms. Among genera are *Acacia*, *Anona*, *Aralia*, *Artocarpus*, *Avicennia*, *Banisteria*, *Bumelia*, *Canavalia*, *Canna*, *Carapa*, *Cassia*, *Cedrela*, *Celastrus*, *Chrysobalanus*, *Cinnamomum*, *Coccolobis*, *Combretum*, *Dalbergia*, *Dodonaea*, *Drypetes*, *Engelhardtia*, *Fagara*, *Ficus*, *Fraxinus*, *Glyptostrobus*, *Guettarda*, *Ilex*, *Inga*, *Juglans*, *Laurus*, *Magnolia*, *Maytenus*, *Myrica*, *Nectandra*, *Nyssa*, *Oreodaphne*, *Oreopanax*, *Osmanthus*, *Paliurus*, *Persea*, *Pisonia*, *Pistia*, *Pithecolobium*, *Planera*, *Porana*, *Prunus*, *Quercus*, *Reynosia*, *Rhamnus*, *Sapindus*, *Sideroxylon*, *Simaruba*, *Sophora*, *Sterculia*, *Taxodium*, *Trapa*, *Zamia*, *Zizyphus*. It is to be noted that some of these genera such as *Glyptostrobus*, *Laurus*, *Oreodaphne*, *Paliurus*, *Porana*, *Sideroxylon* and *Trapa*, are now confined to the Old World.

The Green river beds of the Rocky mountain group belong to a later Eocene age. Knowlton, who revised the flora in 1924, stated that there is an overwhelming preponderance of species with living allies in tropical and sub-tropical regions. He tentatively divided the species into lowland and upland forms. The flora is not a large one. Among the lowland forms he named species of palm, a relation of the banana, and *Brasenia* (a species of water-lily), besides other genera which are the same as some recorded from the Wilcox beds.

**Oligocene.**—The Oligocene is not well known from America. From the coastal region Berry has described several small floras. Among them are those of the Alum Bluff beds and the Catahoula Sandstone. Like so many Oligocene floras in Europe the constituents show mixed relationships. Some, such as palms, show alliance with tropical forms. Others, like *Ulmus*, *Rhamnus* and *Paliurus*, with cooler forms. Berry concludes that the Oligocene

period in America was warmer than the Eocene, although this is open to doubt, for the Oligocene floras are too small to be representative; while the Eocene floras also show a large preponderance of tropical forms. In Europe the Eocene was undoubtedly the warmer period.

**Miocene.**—The Miocene in the south is known only from small floras. Temperate forms mingle with those of a more tropical type, as they do in Europe, indicating a cooler flora supplanting a warmer one, under the influence of a changing climate. The climatic conditions appear to have been very similar to those of the same regions to-day.

In the Rocky mountain region more is known of Miocene floras. The Florissant beds of Colorado, studied by Prof. T. D. A. Cockerell, show beautiful leaf impressions, and recall the Oeningen beds of Switzerland. *Ailanthus*, *Anona*, *Liquidamber*, *Persea*, *Robinia*, *Sequoia*, also persimmon, fig, oak and pine are typical plants. The climate was probably similar to, but damper than, that of the present day.

**Pliocene.**—The Pliocene is not well represented. Its flora is essentially modern, and includes existing species, although a few, like *Trapa* (the water-chestnut), are now extinct in America.

#### CRETACEOUS AND TERTIARY PLANTS OF THE ARCTIC REGIONS

Our knowledge of Arctic plants comes, in the first instance, from the studies made by Heer between 1868 and 1883. He recognized two periods for flowering plants. The older is referred to the Cretaceous. The newer, by him called Miocene, is now generally referred to the Eocene. He described about 335 species from the Cretaceous, and 282 from the Tertiary, but the numbers are certainly far too large, as indicated by Prof. A. C. Seward's work in 1926. The plants come from various localities within the Arctic Circle ranging as far north as Grinnell Land, lat. 81, and Spitzbergen, lat. 79. That the plants are *in situ* is shown by the fact that some are rooted.

**Cretaceous.**—In the lower beds of the Greenland Cretaceous, from Kome, occurs one of the earliest known flowering plants, called by Heer a poplar. From later beds at Atane, besides ferns, some of which are referred to genera now tropical, come many conifers such as *Araucaria*, *Cupressus*, *Sciadopitys* and *Sequoia*, palms, *Artocarpus*, *Liriodendron*, *Magnolia*, *Sapindus*, *Sassafras*, *Rhus*; species referred to Proteaceae and Menispermaceae; also species of oak, poplar and fig. Still higher beds at Patoot contain *Acer*, *Acerates*, *Aralia*, *Zizyphus*, also species of fig, walnut, plane and buckthorn, among flowering plants; and *Dammara* among conifers.

**Eocene.**—The late Prof. Nathorst stated that the Eocene beds of Spitzbergen yield *Taxodium*, *Sequoia*, *Libocedrus*, grass, sedges, pines, willows and pond-weed. From Cape Lyell he recorded *Sequoia*, *Grewia*, *Magnolia*, water-plantain, maple, poplar, willow, alder, birch, hornbeam, hazel, beech, oak, elm, plane and lime.

From Greenland Heer recorded *Ginkgo*, *Libocedrus*, *Glyptostrobus*, *Taxodium*, *Sequoia*, *Pinus* among conifers; *Sassafras*, *Acerates*, *Nyssa*, *Vitis*, *Acer*, *Koelreuteria*, *Juglans*, *Rhus*, and many catkin-bearing trees among flowering plants. The climate was temperate.

Most of these genera reappeared in the Tertiary of Europe and America. They are related to plants now living in Asia and America. Some also live in Europe. The occurrence of these plants within the Arctic Circle has a most important bearing upon the interpretation of plant-history in the Northern Hemisphere.

#### TERTIARY PLANTS IN RELATION TO WORLD HISTORY

**Summary.**—The Tertiary floras of Europe, America and the Arctic, and the living floras of the Far East and North America, are all intimately related. What little is known of the Tertiary floras of Russia and Asia indicates that they, too, were related. It follows that Tertiary floras of an east Asian-American alliance lived on to form the source of much of the living floras of east Asia and America, but were killed in Eurasia. In those regions where they lived, there are no transcontinental mountain-chains forming barriers between the Pole and the Equator, whereas in



the regions where they died, there are. Further, the mountain-chains were being formed whilst the extermination was in progress, and the extermination was greatest after they were formed. Hence it may be inferred that the mountain-chains helped to kill. There is another set of facts which points to the same conclusion. In the early Tertiary, the European flora showed considerable alliance with Indian and African plants, indicating passage between these regions. Later, at the time when the barrier was in existence, the alliance died out. Again, therefore, the barrier would seem to have helped to kill. Alliances must indicate either linkages through some common source, or direct linkage. Also, if the allies are far removed, they must indicate migration. The interruption of the alliances by east-west barriers must indicate that the migration was north-south. Finally the presence of ever cooler and cooler forms must indicate that it was from north to south.

**Explanation.**—The phenomena involved are of world-wide significance, not localized. The best explanation is that originally suggested by Saporta. It meets all the facts, and is based on the assumption that whilst the temperature of, at least, the northern portion of the Northern Hemisphere underwent change, no change, or but very slight, took place in the position of the Poles. As the full measure of the relationship with plants of the Far East has become better known, the evidence supporting this explanation has become more full and definite. The explanation is that in Cretaceous and early Tertiary times the North Polar regions supported a warm type of vegetation, allied to living plants. In the Cretaceous these were of a sub-tropical or warm-temperate type; in the Eocene of a cooler type, at which time the flora of Britain and France was tropical. Slowly the climate cooled, and as it did so, plants migrated southward throughout Europe, Asia and North America, their places being taken by others of a cooler type. These new forms must have been evolved in the north since the linkage of floras continued throughout the Tertiary. The migrants must have suffered loss by the way and undergone evolutionary changes even in America and east Asia, for, although allied to one another, the living floras of these regions differ. Some elements were lost here, others there. In Europe and western Asia the whole were ultimately destroyed. With the ever increasing cold behind, and the impassable mountains in front, they perished, leaving scarcely a trace.

Space will not permit us to enter into any full discussion of the recurrence of Glacial and inter-Glacial periods and influence on the flora. It is evident, however, that if climatic alterations, such as those described, are part of the normal routine that has gone on through all geological periods, and are not merely confined to the latest, then such changes must evidently have had great influence on the evolution and geographical distribution of species and of floras. Whether this was so is a question to be decided, for in dealing with extinct floras it is difficult to decide, except in the most general way, to what climatic conditions they point. We seem to find indications of long-period climatic oscillations in Tertiary times, but none of the sudden invasion of an Arctic flora, like that during more recent times.

It might appear from the above that the Eurasian continent was gradually depleted of plants. This was not so. The flora was greatly impoverished, and has remained so, in contrast to that of America, and especially to that of the Far East. But new plants came in to form the living flora of Eurasia. Where they came from is not certain. Some may have come from the north, but many, possibly most, appear to have come from the vast highlands of central Asia. Their history has yet to be discovered.

#### QUATERNARY PLANTS

The latest chapters in the history of our planet belong to the Quaternary period, and to these chapters plants contribute a very important share. We confine our attention to the Quaternary of Europe, because from it comes almost the whole of our information. The most important feature so far disclosed in the Quaternary of America is the presence of a few east Asian or

European plants—*Xanthium*, *Pterocarya*, cinnamon and laurel, which died out later.

Compared with the Tertiary, the Quaternary period was short—a few hundred thousand years. The important facts regarding it are: (1) In north Europe a series of rapid and marked climatic changes. (2) Throughout the period man is known to have lived.

With the Quaternary ice age, the cooling of the northern regions, which had been going on since the Eocene, reached a climax. The ice age was not a period of unbroken Arctic cold. This is shown by beds of temperate plants intercalated between others showing cold conditions. Such temperate, interglacial beds have been found through north Europe, including Britain. Most of the plants now live in these regions; a few are extinct: others survive elsewhere. The British plants indicate a climate about as warm as, but drier than, at the present day.

In beds of preceding and succeeding age colder types of plants occur. Dwarf Arctic willow and Arctic birch flourished on the plains of Germany and in the south of England. The ground was gay with Arctic and alpine flowers—*Primula farinosa*, *Saxifraga oppositifolia*, *Dryas octopetala*, the alpine poppy, flax, potentilla, geranium, scabious, campanula, gentian and bearberry. *Ranunculus hyperboreus*, one of the most Arctic of buttercups, grew in the Isle of Wight. It now lives no further south than the Dovrefjeld mountains, Lapland, Alaska and Labrador. These changes were going on whilst palaeolithic man lived in Europe.

Subsequently the climate ameliorated. The snow and ice retreated, although slight alternations of climate still occurred. Some of these have been traced by the statistical study of pollen in peat. Using this study for the investigation of peat dredged from the floor of the Dogger Bank, 60 ft. beneath the sea, Dr. G. Erdtman, of Stockholm, discovered that it belonged to the "boreal" period, when the climate was cold but not arctic. The peat had previously been studied by the Reids who found evidence of a great fenland stretching from England to the Continent. The "boreal" period which saw this fenland in existence belongs to the age of early Neolithic man. In Neolithic deposits various cultivated plants are found: wheat, barley, millet, apples, pears, the opium poppy and flax.

As prehistory passes into history we glean interesting scraps of information. Tutankhamun was buried with a string of seeds from the magic mandrake around his neck; the Celts grew wheat, barley and beans at Glastonbury; the Romans brought coriander, fig, grape to Silchester, also vegetables and wild fruits.

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(E. M. R.; M. E. J. C.)



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